Personality Structure and Social Style in Macaques

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Abstract

Why regularities in personality can be described with particular dimensions is a basic question in differential psychology. Nonhuman primates can also be characterized in terms of personality structure. Comparative approaches can help reveal phylogenetic constraints and social and ecological patterns associated with the presence or absence of specific personality dimensions. We sought to determine how different personality structures are related to interspecific variation in social style. Specifically, we examined this question in six different species of macaques, as macaque social style is well characterized and can be categorized on a spectrum of despotic (grade 1) versus tolerant (grade 4) social styles. We derived personality structures from adjectival ratings of Japanese (*Macaca fuscata*; grade 1), Assamese (*M. assamensis*; grade 2), Barbary (*M. sylvanus*; grade 3), Tonkean (*M. tonkeana*; grade 4), and crested (*M. nigra*; grade 4*)* macaques and compared these species to rhesus macaques (*M. mulatta*; grade 1) whose personality has previously been characterized. Using a non-parametric method, fuzzy set analysis, to identify commonalities in personality dimensions across species, we found that all but one species exhibited consistently defined Friendliness and Openness dimensions, but that similarities in personality dimensions capturing aggression and social competence reflect similarities in social styles. These findings suggest that social and phylogenetic relationships contribute to the origin, maintenance, and diversification of personality.

Keywords: animal personality, Old World monkey, social style, fuzzy set, comparative, dominance

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…there are an infinite number of personality traits one can define and measure, but evolutionarily analyzable order will tend to be found only in those causally related to adaptive function. (Tooby & Cosmides, 1990, p. 25)

Broad support exists for basic personality dimensions related to sociality, anxiety, and cooperativeness in a variety of distantly related animal taxa, ranging from octopuses to chimpanzees (Gosling & John, 1999). The five human factors of Neuroticism, Extraversion, Openness, Agreeableness, and Conscientiousness are thought to be nearly ubiquitous features of human dimensions (McCrae & Costa, 1997) though findings in small-scale societies (Gurven, von Rueden, Massenkoff, Kaplan, & Lero Vie, 2013) suggest that personality structure may sometimes differ between human populations. A basic question in personality psychology is why humans exhibit the particular number and composition of personality dimensions that they do (Fiske, 1994).

One way to approach this question is to compare personality traits between closely related species. Behavioral traits show as strong a phylogenetic signal as morphological traits (de Queiroz & Wimberger, 1993), meaning that closely related species are more similar because they inherited traits from a common ancestor. Species may also be distinguished by between-individual variability of behaviors (Gosling & John, 1999) and a species' personality structure is the total configuration of this behavioral variation, including the presence/absence of variation in low-level dispositional traits (or facets) as well as the correlations among facets into higher-order personality dimensions. Finding similarities and differences in personality structure at different points in the tree of life (e.g., humans versus chimpanzees,

apes versus Old World monkeys) can lend insight to the social and ecological conditions that accompanied the emergence of each personality dimension (Gosling & Graybeal, 2007) and differentiate analogous, independently evolved personality features from those that are homologous and inherited from a common ancestor (Harvey & Pagel, 1991). Phylogenetic analysis is highly informative of function in social and personality psychology because it can reveal the evolutionary history of the co-occurrence of behaviors (Fraley, Brumbaugh, & Marks, 2005; Gosling & Graybeal, 2007). Analogues of the five factors, along with the dimensions Dominance and Activity, have been found in nonhuman primates, although species differ in the personality dimensions they exhibit (Freeman & Gosling, 2010). Within at least one nonhuman primate species, i.e., chimpanzees, personality structures derived from rater assessments are relatively invariant across habitats, rearing environments, social groups, and observers' cultures (Pederson, King, & Landau, 2005; Weiss et al., 2009; Weiss, King, & Hopkins, 2007); and chimpanzee personality dimensions differ from those exhibited by other primate species (Morton et al., 2013; Weiss, Adams, Widdig, & Gerald, 2011; Weiss, King, & Perkins, 2006). Although these comparisons do not rule out more delicate variation in personality structure within these species and populations, they indicate that species can be consistently described and differentiated from each other in terms of broad personality dimensions despite their wide-ranging differences in social structure and ecological conditions (Boehm, 1999) where even small ecological differences between populations may contribute to behavioral differences in the same species (Humle & Matsuzawa, 2002). Given that species can be distinguished on the basis of personality traits that are exhibited in a broad range of contexts, it would be reasonable to expect (but not assume) that phylogenetic affinity would be reflected in species personality structures (Weiss & Adams, 2008).

Variation in human personality has been explained as adaptations for alternative behavioral strategies (Buss, 1991; MacDonald, 1995; Nettle, 2011), including social

behaviors (e.g., mate selection and alliance formation). Given the trait-like persistence of personality and our shared evolutionary history, it is reasonable to expect that such an adaptive explanation could also apply to accounts of personality differences in nonhuman species. For example, the presence of a Conscientiousness dimension in humans (Digman, 1990) and chimpanzees (King & Figueredo, 1997) but not in orangutans (Weiss et al., 2006) or rhesus macaques (Weiss et al., 2011) suggests that this dimension is an evolutionary derived feature in the human–chimpanzee lineage relative to the ancestral condition (Weiss et al., 2011). A similar personality domain, Attentiveness, also appears to have evolved independently in brown capuchins (Morton et al., 2013), a New World monkey species that behaviorally resembles chimpanzees in many ways (Fragaszy, Visalberghi, & Fedigan, 2004).

As these broad brush strokes are being applied, a complete picture is beginning to emerge. This picture illustrates the existence of personality differences between species, with an overall pattern suggesting that species-specific personality structures, despite their multifactorial complexity, can be traced phylogenetically (King & Weiss, 2011). Moreover, as variation in social organization, or the number of same- and opposite-sex pairs in a group (Shultz, Opie, & Atkinson, 2011), and social structure, or the style of social relationships within a group (Thierry, Iwaniuk, & Pellis, 2000), is conserved within primate lineages it may be possible to uncover relationships between social structure and expected differences in personality structures across primate lineages.

To compare differences between species in features of personality structure --- such as the presence or absence of personality domains or which facets of personality cluster together --- it is most fruitful to compare species that are closely related, but vary in high-level ecological or life-style patterns (Carter & Feeney, 2012; Mettke-Hofmann, Ebert, Schmidt, Steiger, & Stieb, 2005). Because macaques (genus, *Macaca*) serve as a model for

understanding variation in social structure (Thierry, Singh, & Kaumanns, 2004), they represent an ideal taxon for testing whether personality dimensions are adaptations to aspects of social structure. Macaques belong to the taxonomic family Cercopithecidae (Old World monkeys) that shared a common ancestor with humans around 29 million years ago (Andrews, 1986; Chatterjee, Ho, Barnes, & Groves, 2009). Macaques are a relatively species-rich genus, consisting of around two dozen species that reside in a range of habitats and ecologies, making them the most geographically distributed primate genus next to humans (Fleagle, 1999; Melnick & Pearl, 1987).

In primates, there is great variation between species in social structure, which refers to the pattern of social interactions and the resulting relationships, including dominance style (Kappeler & van Schaik, 2002). For macaques, species that share a recent common genetic ancestry (that is, they are phylogenetically more closely related) tend to exhibit similarities in their social structure (Balasubramaniam et al., 2012; Thierry et al., 2000). Social structures of macaque species can be classified along a four-category spectrum of social styles based on how strict or relaxed their female dominance hierarchies are (Thierry, 2000) and on how traits related to aggression and conflict management covary (Thierry et al., 2007). On one end of the spectrum, grade 1 species such as rhesus macaques show strong nepotism and agonistic outcomes are highly asymmetrical. In these societies females show a very strong bias towards kin and individuals of higher dominance rank are almost always able to get their way when faced against subordinate individuals. On the opposite end of the spectrum, grade 4 species such as the crested macaque (*M. nigra*) are more egalitarian. In these societies, social interactions are more symmetrical and conciliatory behaviors between maternally unrelated females are more frequent. Grades 2 and 3, which include species like long-tailed (*M. fascicularis*) and bonnet (*M. radiata*) macaques, exhibit an intermediate degree of social tolerance between these extremes. Such classification of female dominance relations may not

always generalize to dominance styles among male members of a species, which are known to even exhibit the opposite patterning (Cooper & Bernstein, 2008; Preuschoft & Paul, 2000; Richter, Mevis, Malaivijitnond, Schülke, & Ostner, 2009; Schülke & Ostner, 2008; but see Thierry, 2004).

For the present study, we sought to evaluate the theoretical expectation that personality is co-adapted with social strategies by assessing whether personality structure of macaque species can be explained by a species' social style classification. The theory that personality adaptations are linked to social style and its underlying mechanisms has two initial hurdles to clear. The first is that closely related species will be more likely to have similar personality dimensions because they have inherited both personality structure and social style from a common ancestor. A lack of close concordance in personality structure between closely related species would rule out a strong link between personality and social style. Second, more distantly related species with similar social styles should share features of their personality dimensions. To evaluate these predictions, we tested the relationship between macaque personality structure and social style in five macaque species representative of the entire despotic-egalitarian spectrum. To these ends, we collected data on Japanese (*M. fuscata*), Barbary (*M. sylvanus*), Assamese (*M. assamensis*), Tonkean (*M. tonkeana*), and crested macaques (*M. nigra*) and compared their personality structures to the published personality structure of rhesus macaques (Weiss, Adams, Widdig, & Gerald, 2011).

To address this question, our first goal was to derive personality structures for the Assamese, Barbary, crested, Japanese, and Tonkean macaques. Previous studies of macaque personality, including rhesus (Bolig, Price, O'Neill, & Suomi, 1992; Capitanio, 1999; Stevenson-Hinde, Stillwell-Barnes, & Zunz, 1980; Stevenson-Hinde & Zunz, 1978; Sussman, Ha, Bentson, & Crockett, 2013; Weiss et al., 2011), lion-tailed (Rouff, Sussman, & Strube,

2005), long-tailed (Sussman et al., 2013; Uher, Werner, & Gosselt, 2013), Barbary (Konečná, Weiss, Lhota, & Wallner, 2012), crested (Neumann, Agil, Widdig, & Engelhardt, 2013), pig-tailed (Sussman et al., 2013), and Tibetan macaques (Pritchard, Sheeran, Gabriel, Li, & Wagner, 2014) have used differing questionnaires, behavior lists, and experimental tests. This variety limits cross-species comparability. To maximize our ability to compare species, we used the same personality instrument for each species so that differences in structure would reflect species or sampling characteristics rather than method variance (Campbell & Fiske, 1959; King & Weiss, 2011; Weiss, Inoue-Murayama, King, Adams, & Matsuzawa, 2012).

Our second goal was to determine the extent to which personality dimensions overlapped across these species and whether any of the personality dimensions were consistent with those previously identified in rhesus macaques (Confidence, Friendliness, Dominance, Openness, Anxiety, and Activity) (Weiss et al., 2011). If macaque species are not similar to each other in some aspect of personality structure compared with other primate species, then personality is unlikely to be related to social style. Despite the difficulties of using personality instruments that have been incompletely adapted from other species (Uher, 2008) and the history of assigning various labels to macaques' personality resulting in a differing number of components, many of these personality constructs tap into the same or similar dimensions, which suggests that labeling differences are more of a semantic issue. Both rhesus (Weiss et al., 2011) and Barbary macaques (Konečná et al., 2012) exhibit a Friendliness dimension, which combines elements of great ape Extraversion and Agreeableness (King & Figueredo, 1997; Weiss et al., 2006), so we examined whether similar dimensions were present in the other macaque species. Earlier studies of rhesus macaques (Bolig et al., 1992; Capitanio, 1999; Stevenson-Hinde & Zunz, 1978) did not find any dimension resembling Openness, but this can be considered a methodological issue, because when personality was assessed with a broader instrument, which had previously

uncovered this domain in chimpanzees (King & Figueredo, 1997), Openness was revealed for both rhesus and Barbary macaques (Konečná et al., 2012; Weiss et al., 2011). As such, we sought to determine whether the same broad questionnaire would uncover Openness in other species of macaques. Rhesus macaques also have three (Dominance, Confidence, and Anxiety) and Barbary macaques two (Confidence and Opportunism) separate domains, which share facets in common with Dominance and Neuroticism, in apes (King & Figueredo, 1997; Weiss et al., 2006). We therefore sought to determine how consistent this separation of dimensions is with other macaque species.

Our third goal, the central goal of our study, was to evaluate the competing hypotheses as to whether the presence or absence of certain dimensions is related to social style, particularly, those involved in dispositions for interacting with social partners (namely, the Dominance, Opportunism, and Friendliness dimensions found in rhesus and Barbary macaques) or whether phylogenetic proximity alone can explain species similarity. A cladogram (Figure 1) shows the phylogenetic relationships among the six species, which shared a common ancestor approximately 9 million years ago (Chatterjee et al., 2009; Perelman et al., 2011), contrasted with their similarities in terms of social style. Rhesus and Japanese macaques are classified as grade 1 and exhibit highly asymmetrical dominance encounters. With an intermediate steepness in their dominance hierarchies, Assamese macaques are classified as grade 2 and Barbary macaques as grade 3. The much more egalitarian crested and Tonkean macaques are grade 4 (Thierry, 2000, 2007). Because Japanese and rhesus macaques are both grade 1 species, we hypothesized that if Japanese macaques did not most resemble rhesus macaques in exhibiting a Dominance dimension and in lacking a separate dimension for Opportunism (Konečná et al., 2012) then personality was unlikely to be a reflection of social style adaptations. Likewise, we hypothesized that the most egalitarian species (crested and Tonkean macaques) would be more similar to each

other and that Assamese and Barbary macaques would be intermediate between the less egalitarian and more egalitarian macaque species. By contrast, if personality is unrelated to social style, then the most egalitarian species (crested and Tonkean macaques) would be expected to be more similar to their closer phylogenetic relatives---the less-egalitarian Assamese, Japanese, and rhesus macaques---than to the relatively egalitarian Barbary macaques. Because similarity in social style tracks phylogeny in macaques (Balasubramaniam et al., 2012), it is not possible to test the explanation that social style is the only driver of species differences in personality features but species comparisons can rule its influence out. Species similarity that matches the phylogeny would tell us when each personality dimension emerged (Gosling & Graybeal, 2007; Weiss et al., 2011). Lack of resemblance between these species would be the result of evolutionary divergence through species-specific adaptations or genetic drift (Harvey & Pagel, 1991). Finally, the finding of a lack of consistency between personality dimensions with either social style or phylogeny could be interpreted as artifacts of rater assessment (Uher et al., 2013; Weiss et al., 2012).

Our fourth goal was to test whether personality scores differed between females and males, depending on species-specific differences in social style. When measured with behavioral tests, rhesus macaque (grade 1) females, rhesus males, and long-tailed macaque (grade 2) males made the most threat displays while pigtailed macaque (grade 2) males made the least. Female long-tailed and pigtailed macaque made an intermediate number of threat displays (Sussman et al., 2013). We thus predicted that females in species with more egalitarian social styles would score, in comparison with males of the same species, relatively lower in dimensions encompassing assertiveness, aggressiveness, and alliance formation (e.g., Dominance, Opportunism); and higher in dimensions related to social affiliation (e.g., Friendliness).

Methods

Subjects

The Japanese macaque sample consisted of 74 subjects of two subspecies: 24 from a free-ranging troop in Japan (Koshima), 21 from two wild troops on Yakushima, Japan (Umi and Donguri), and 29 from two zoological parks in Italy and the United States. The two wild troops from Yakushima were of the subspecies *M. f. yakui* while the other individuals were all of the subspecies *M. f. fuscata*. The Barbary macaque sample consisted of 74 subjects from three wild troops (Flat-face, Green, and Large) living in the Middle Atlas Mountains, Morocco (Majolo, McFarland, Young, & Qarro, 2013). The Assamese macaque sample comprised 60 subjects from a wild troop living in a natural habitat at the Phu Khieo Wildlife Sanctuary, Thailand (Fürtbauer, Schülke, Heistermann, & Ostner, 2010; Ostner, Vigilant, Bhagavatula, Franz, & Schülke, 2013). The Tonkean macaque samples comprised 46 subjects from five groups. Four of the groups were located in large enclosures at the Parco Faunistico di Piano dell'Abatino Rescue Center in Italy. The fifth group lived in a 1-ha wood park at the Primatology Center of Strasbourg, France. The crested macaque samples comprised 53 subjects from five wild groups (PB, R1, R2, R3, and R4) living in the Tangkoko Reserve, Sulawesi, Indonesia (Duboscq et al., 2013). The rhesus macaque sample was drawn from a study of rhesus macaque personality (Weiss et al., 2011), where data was collected on 125 free-ranging subjects from three social groups (R, S, and V) living in Cayo Santiago, Puerto Rico. Where exact ages were not known, subjects were categorized into general age classes by the field researchers (Bissonnette, de Vries, & van Schaik, 2009; Tarnaud & Hernandez, 2007). Based on sexual maturation and life history stages (Fooden & Aimi, 2005), we classified macaques as infants (0-1 years old), juveniles (2-6 years old), adults (7-14 years old), or senior adults (15+ years old). Samples sizes for each age group are listed in Table 1.

Instruments

Personality. We measured the personalities of subjects using the 54-item Hominoid Personality Questionnaire[1] (HPQ; King & Figueredo, 1997; Weiss et al., 2009). The HPQ is an expanded version of the 43-item Chimpanzee Personality Questionnaire (King & Figueredo, 1997). Each item consists of an adjective and one to three sentences that define the adjective within the context of general behaviors common to primates, rather than behaviors specific to chimpanzees. For example, 'fearful' is defined as "Subject reacts excessively to real or imagined threats by displaying behaviors such as screaming, grimacing, running away or other signs of anxiety or distress." The derivation and sources of the HPQ items are detailed in the Supplementary Material.

Ratings

Raters were zookeepers, field station staff, and researchers who were familiar with the subjects they rated, on an individual basis. Raters had between 4 months and 6 years (mean = 22.5 months, *SD* = 17.9 months) experience with each of the subjects they assessed. The total number of raters and raters/subject for each sample is listed in Table 1. For Japanese macaques, one rater used a Japanese-language version of the questionnaire (see Weiss et al., 2009 for a description of how questionnaires were translated) while the remaining seven used the English-language version. Ratings were made between February 2009 and February 2010. For the Barbary macaques, six raters used the English-language questionnaire and ratings were made between June 2009 and June 2011. For Assamese macaques, six raters used a Thai version of the questionnaire and two used the English-language questionnaire. Ratings were made between May and December 2009. The crested macaques were rated at two time points: between July and October 2009 and between July and September 2014. Ratings of the

[1]The Hominoid Personality Questionnaire can be obtained from http://extras.springer.com/2011/978-1-4614-0175-9/

Tonkean macaques were made at two time points: one group was rated between January 2008 and May 2009; a second groups was rated in May 2013. Information on rater characteristics for the rhesus macaque sample can be found in Weiss et al. (2011). There was some missing data: four Barbary, nine Assamese, and one Tonkean macaque subject were each missing a rating on one personality item.

Analyses

Item reliabilities. We used two intraclass correlation coefficients or *ICC*s (Shrout & Fleiss, 1979) to assess item reliabilities. *ICC*(3, 1) gives the expected correlation of item scores between single raters assessing the same subject. *ICC*(3, *k*) gives the expected correlation among the mean item scores of two groups of *k* raters. Items with zero or negative reliabilities were excluded from further analyses.

Data reduction. We used principal components analysis (PCA) to determine the dimensions underlying the data separately for the Japanese, Assamese, Barbary, and Tonkean samples. We selected PCA instead of principal axis factor analysis because the purpose of this analysis was to cluster items into domains rather than to estimate exact factor loadings. Furthermore, structures derived from PCA are similar to those derived from principal axis factor analysis (Velicer, 1977) and previous studies of primate personality have found that the structures yielded by the two techniques are almost identical (Weiss et al., 2011; Weiss et al., 2006). We computed PCAs using the principal procedure in R (Revelle, 2011). To determine the number of components to extract for each sample, we examined the scree plot and conducted a parallel analysis using the paran function in R (Dinno, 2008), which determines the number of components by the number of eigenvalues that are greater than what would be expected by chance correlations among the items (Horn, 1965). We ran the PCA on monkeys' item scores averaged across raters. Because the Crested and Tonkean macaque sample had

fewer subjects than items, we smoothed the among-item correlation matrix to make it positive definite (Bates & Maechler, 2013). We obtained orthogonal components using a varimax rotation and oblique components using a promax rotation.

We interpreted personality dimensions on the basis of the item content and pattern of loadings which yielded the rhesus macaque and ape personality structures (Weiss et al., 2011). We created unit-weighted domain scores for each individual, which assigns items with salient loadings (defined as $\geq |.40|$) to a component score of either +1 or −1 depending on the direction of the loading, based on their species' structure. Items that did not have a salient loading were assigned a component weight of 0. We used unit-weighting to create more generalizable results as scores derived from differentially-weighted loadings are known to vary across samples (Gorsuch, 1983). Domain scores were computed as the average of the items (reverse coded as needed) that each individual was scored on, to handle the few missing scores. We also created unit-weighted domain scores based on the rhesus macaque, chimpanzee, and orangutan personality dimensions and examined the correlations with domain scores from each species' structure. This scoring approach had the advantage over calculations of congruence coefficients between components because it did not require the personality structures to contain the same items. We also calculated the inter-rater reliabilities of domain scores using *ICC*s and internal consistencies using Cronbach's alpha.

Fuzzy set analysis. King and Weiss (2011) point out that, although the items making up a domain will vary among species, individual domains within a species are still distinct from other domains. A domain can therefore be conceptualized as a "fuzzy set" of items. Rather than yes/no inclusion, a fuzzy set defines the continuous probability of each item being included in a set (Smithson & Verkuilen, 2006; Zedeh, 1965). This property of membership is referred to as *degree-vagueness*. In fuzzy set theory, a membership function is used to assign an object (in this case, a personality item) to a set (a personality domain). The

membership function maps the object onto the unit interval, from 0 to 1 (Smithson & Verkuilen, 2006), as follows:

$$m_K(i) : H \rightarrow [0,1] \quad (1)$$

H is space of HPQ items, *H*= *fearful*, *dominant*, *persistent*, …, *independent*, and $m_K(i)$ is the mapping function of item *i* onto personality dimension *K*. Because the loading of an item onto a personality component (v_i) is between -1 and +1 we used a mapping function of the absolute value of the loading:

$$m_K(i) = |v_i| \quad (2)$$

While many other membership functions are possible (for example, ones that have a natural interpretation of the probability that a particular item is part of each personality dimension), we used the mapping in Equation 2 so that outputs of the set functions can be understood as loadings.

The shared support that each item has for two or more personality domains from different species can be determined by making a fuzzy intersection between the sets, where a set contains information on the membership of each item in a personality domain. As described in Equation 3, membership of an item in the fuzzy intersection between two personality domains *X* and *Y*, $X \cap Y$, is:

$$m_{X \cap Y} = \min(m_X, m_Y) \quad (3)$$

which in effect gets the lowest loading (or, more precisely, the value closest to 0) of each item on the two components. We used a permutation test to determine a cutoff for the salient inclusion of an item in a fuzzy set. We did this by randomly selecting one domain from each species and calculating the fuzzy intersection of the five domains. We repeated this procedure 100 times to generate a null distribution of item membership then calculated the 95th percentile as the cutoff. We assessed the relationship among semantically similar domains of each species in terms of the shared support of their items. We suggest that the fuzzy sets that

are identified describe lower-order facets of personality that are aggregated together in different combinations to compose the higher-order dimensions that differ between species.

Personality structure comparisons. To compare structural differences in personality between species, we created two metrics based on the fuzzy sets that were identified. The first measured the independence of fuzzy sets with overlapping item membership. For example, for three species (X, Y, and Z) we might define a fuzzy set $m_A = X_1 \cap Y_1 \cap Z_1$ using the species dimensions describing social dominance. Furthermore, suppose that in species X and Y items related to aggressiveness are in this first dimension but in species Z are part of a separate dimension, Z_2; a fuzzy set would then be defined as $m_B = X_1 \cap Y_1 \cap Z_2$. Because of how they were composed m_A and m_B will contain some items in common, e.g. 'bullying'. Thus in species X and Y m_A and m_B are part of the same personality dimension while in species Z they make up two separate dimensions. However, because of the item overlap, the two fuzzy dimensions will overlap to some extent in all species. One gauge of how much m_A and m_B describe the same versus different dimensions in a particular species is how perpendicular the loadings are to the same set of items if those items loaded only on a single dimension. To do this we first took the loadings of the combined salient items $m_A + m_B$ on the dimension that was used to define m_A (e.g, for species X this is X_1). We then found the dimension from species X apart from X_1 that had the highest total loadings on items $m_A + m_B$ (call this dimension X_j). For each item x we can define a vector $\mathbf{a} = [x_1, xj]$ from the loadings of that x on X_1 and X_j. We can then calculated a version of the cross product (which is a function of both the angle between two vectors and their sizes) between **a** and a hypothetical item rotated to load only on X_1, namely $\mathbf{b} = [\sqrt{}(x_1^2 * x_j^2), 0]$. This cross product is $\mathbf{a} \times \mathbf{b} = x_1^2 x_j^2 |\sin(\tan(x_1, xj))|$. That is $\tan(x_1, xj)$ calculates the angle θ between **a** and **b**. If the item only loads on X_1 then $|\sin(\theta)|$ will be zero and if it only loads on X_j then it will be 1; this is then weighted by the length of the vectors $x_1^2 x_j^2$. Finally, we define the amount of independence

between $m_A + m_B$ as $m_A \times m_B = \text{var}(\mathbf{a} \times \mathbf{b})$, or the variance in the cross products of all the items. That is $m_A \times m_B$ is minimized when all the items load only on a single dimension and maximized when some of the items have large loadings on separate dimensions. We used this metric for item groupings that seemed to have different configurations across species. When a fuzzy set was made up of dimensions that seemed to have a consistent definition across species, we created a second metric that was the first eigenvalue of the matrix of correlations between ratings on those items in each species. This can be thought of as the size of a fuzzy set, so we refer to it as $\|m_A\|$.

Using these metrics, we then clustered the species based on high-level personality structure similarity. First, within each metric we ranked the species from 1 to 5 so that each metric contributed equally to species similarity calculations. Using all the metrics we measured the Manhattan distance between each species (the total number of differences in rank between them) and then made a hierarchical clustering using R (R Development Core Team, 2014). Species that were more similar in terms of the metrics would be clustered together.

Species domain score comparisons. To compare sex differences in personality domains to social style, we created domain scores for each personality dimension discovered in the fuzzy set analysis. Item scores for each subject were first averaged across raters. We calculated differentially weighted domain scores using the membership (loading) of each item in the set so that items that were more highly correlated with the latent factor in all species were given more weight. We standardized domain scores within each species so that the size of sex differences could be compared across social styles. We then used a linear mixed effects model (Bates & Maechler, 2010) to estimate mean differences in personality scores between sex, age class, and social grade and to test for a Sex × Social Grade interaction for fuzzy personality domains related to Dominance, Opportunism, and

Friendliness; dispositions which relate to social interactions. The fixed effects in the model were sex (coded female = 1, male = -1), age class (coded infant = 1, juvenile = 2, adult = 3, senior = 4), and social grade for each species (coded rhesus, Japanese = 1; Assamese = 2; Barbary = 3; crested, Tonkean = 4). Troop ID was included as a random effect to remove mean differences between study sites and social groups for a given species.

Visual inspection of plots of the variance of domain scores suggested species-by-sex differences in variance of scores. Given that the amount of within-species variation can also be used to compare personality across species (Carter & Feeney, 2012), we first removed within species variance attributable to factors other than sex. Separately for each species we regressed personality scores on age category (infant, juvenile, adult, and senior adult) and troop ID. For each regression we extracted and standardized the residuals and calculated the variance in the residuals for females and males. We tested for sex differences in variance within each social grade using a permutation test, randomly permuting the sex identifiers and recalculating the difference in variance. We conducted 1000 permutations of sex to create a null distribution against which the actual differences in variance could be compared.

Results

Goal 1: Characterization of personality

Data reduction. Although item reliabilities ranged considerably (see Table 2), overall reliabilities were acceptable. Full item reliabilities are given in Table S1. From principal components analyses of the retained items, the dimensions for each species were only weakly intercorrelated, with most correlations not greater than |.30| (see Table S2). We therefore used the loadings from the orthogonal (varimax) rotations. Parallel analysis suggested that each species' (Japanese, Barbary, Assamese, crested, and Tonkean macaque) personality could be described by between four and five dimensions (see Figure 2 and Table 3; Tables S2-S6 in

the Supplementary Material provide full descriptions and item loadings for all personality dimensions).

Domain reliabilities. For assessing inter-rater reliabilities, we calculated domain scores using unit-weighting on each rater's assessment of each of the subjects. For Japanese macaques, the inter-rater reliabilities of mean ratings ranged from poor (.45 for Friendliness) to good (.79 for Anxiety). Interrater reliabilities for Barbary macaques ranged from poor (.58 Irritability) to good (.78 Friendliness). For the Assamese macaques, reliabilities ranged from poor (.68 Openness) to excellent (.89 for Confidence). Mean ratings reliabilities for crested macaques also ranged from poor (.59 for Aggressiveness) to excellent (.87 for Friendliness). Domain scores for all of the Tonkean personality dimensions showed good interrater agreement (> .8). We calculated internal reliabilities for personality scores via Cronbach's alpha. Overall internal consistency was good (see Table S8).

Goal 2: Species similarity and variation in personality

Like rhesus macaques (Weiss et al., 2011), personality dimensions related to affiliative behaviors (labeled Friendliness) and curiosity (labeled Openness) appeared as separate dimensions in four out of the five macaque species that we sampled (see Figure 2 and Table 3). By contrast, macaque species differed with respect to the composition of personality items that describe aggression and social competence. For Japanese and Tonkean macaques, these items loaded on a single component, labeled Dominance. In Barbary, Assamese, and crested macaques these items were split between separate dimensions. In all three of these species, items related to dominance and submission loaded on dimensions that we labeled Confidence. Items related more to aggression and bullying loaded on components that we labeled Irritability in Barbary macaques, Opportunism in Assamese macaques, and Aggressiveness in crested macaques (see Supplementary Information).

Personality domains as fuzzy sets. The examination of item content and unit-weighted domains scores showed that distinct Friendliness and Openness domains exist across macaque species, but that macaques differ in the composition of the other personality domains. We named the fuzzy sets for each domain as follows: *D* = dominance, *C* = confidence, *F* = friendliness, *G* = aggressiveness, *O* = openness, *X* = anxiety, and *P* = opportunism. We used the subscripts *r*, *j*, *b*, *a, c,* and *t* for rhesus, Japanese, Barbary, Assamese, crested and Tonkean macaques, respectively and the subscript *M* for all macaques. For example, D_M or "Dominance-M" is the fuzzy intersection of macaque Dominance-like or Dominance-including domains. The 95th percentile of item memberships from fuzzy intersections among domains randomly selected from each species was $m_K(i) = |.20|$, so we used this value as the lower bound for considering an item as defining a fuzzy set. We used fuzzy set theory to differentiate semantically similar domains (Confidence/Dominance, Dominance/Opportunism/Irritability/Aggressiveness, Confidence/Anxiety) and to determine what items described the domains that were found in all species (Friendliness, Openness) (see Figure 2).

Dominance-M and Confidence-M. Both Dominance and Confidence domains were defined by items related to the negative pole of Agreeableness ('dominant') and the positive pole of Neuroticism ('vulnerable', 'anxious'). We used fuzzy intersection to find items uniquely defining the Confidence and Dominance domains in rhesus macaques, Dominance in Japanese and Tonkean macaques, and Confidence in Barbary, Assamese, and Crested macaques. The fuzzy intersection for Confidence-like domains for macaques, C_M, was

$$C_M = C_r \cap D_j \cap C_b \cap C_a \cap C_c \cap D_t$$

and for Dominance-like domains was

$$D_M = D_r \cap D_j \cap C_b \cap C_a \cap C_c \cap D_t$$

Both Dominance-M and Confidence-M were described by the item 'dominant' (see Figure 3, Table S9). However, the Dominance-M set had a higher loading than Confidence-M on this item (.64 versus .50). Confidence-M set was defined best by the items (not) 'submissive', (not) 'fearful', and (not) 'timid'. It was also different from Dominance-M by having higher membership for the items 'anxious' and 'depressed'. Dominance-M was separable from Confidence-M by items related to aggressiveness and social maneuvering and Machiavellianism ('manipulative', 'aggressive', 'bullying'). This Dominance facet captures aspects of Machiavellian behaviors (Byrne & Whiten, 1997) related to social alliance formation and maintenance. An exploratory analysis of Tonkean Sociability also revealed its similarity to the Confidence domain in other species. Their fuzzy intersection retained salient loadings from (not) 'dependent', (not) 'depressed', 'sociable', (not) 'gentle', 'timid', (not) 'solitary', and 'independent'.

Aggressiveness-M. Barbary, Assamese, and crested macaques had domains (Irritability, Opportunism, and Aggressiveness, respectively) related to the negative pole of Agreeableness and Conscientiousness that defined items related to Dominance in other species. We therefore constructed the intersection:

$$G_M = D_r \cap D_j \cap I_b \cap P_a \cap G_c \cap D_t$$

which had the greatest membership for the items 'aggressive' and 'bullying' (see Figure 3). Aggressiveness-M thus differs from the more inclusive Dominance domain by describing aggression without behavioral aspects related to social potency, such as 'dominant', 'manipulative', and 'independent'.

Anxiety-M. In rhesus macaques the separation between Confidence and Anxiety was described as representing reactions to situation-specific versus more generalized reactions to stressors (Weiss et al., 2011). We looked at the intersection of Anxiety in rhesus and Japanese

macaques with Confidence in Barbary, Assamese, and crested macaques and Dominance in Tonkean macaques.

$$X_M = X_r \cap X_j \cap C_b \cap C_a \cap C_c \cap D_t$$

Both the Confidence-M and Anxiety-M sets were described by the items 'anxious', 'vulnerable', and 'fearful'. Confidence-M included a greater number of items while the anxiety set defined a narrower personality facet. Anxiety-M was also distinguished from Confidence-M by the inclusion of the item 'quitting'.

Friendliness-M. The fuzzy intersection of the Friendliness domains

$$F_M = F_r \cap F_j \cap F_b \cap F_a \cap F_c \cap F_t$$

showed that the items that had good support of Friendliness across species were describing both Extraversion- ('sociable') and Agreeableness-like ('affectionate', 'helpful') facets (see Figure 3). We then intersected the macaque Friendliness set (F_M) with chimpanzee Extraversion (E_{CH}) and Agreeableness (A_{CH}) defined using loadings from a study that used the same HPQ items (Weiss et al., 2009). The chimpanzee/macaque Extraversion set ($F_M \cap E_{CH}$) and Agreeableness set ($F_M \cap A_{CH}$) were both well supported by the item *sociable* but were differentiated by the membership of the other items. As the Tonkean Sociability dimension also had salient loadings from Extraversion-like items, we created a fuzzy intersection between it and Friendliness-M set of the other species. This revealed a facet characterized by 'affectionate', (not) 'solitary', 'sociable', 'friendly' and (not) 'depressed'.

Openness-M. A fuzzy intersection between the Openness domains plus the Friendliness domain of crested macaques

$$O_M = O_r \cap O_j \cap O_b \cap O_a \cap F_c \cap O_t$$

was supported by the membership of a common set of items related to exploratory behavior, such as 'inventive'. The Openness dimensions were also all described by items related to low impulse control ('impulsive', 'erratic').

Goal 3: Social Style, Phylogeny and Personality

To compare species similarity in terms of social style and phylogeny, we first took the loadings of items with membership in pairs of fuzzy sets that had overlapping or semantically similar item content (Dominance-M/Aggressiveness-M, Dominance-M/Confidence-M, and Confidence-M/Anxiety-M) and assessed how much, within a species, the two fuzzy sets defined described the same or separate dimensions. We also calculated a second metric for the sizes of the Friendliness and Openness dimensions, which the fuzzy set analysis showed had consistent definitions across species. We used this metrics to cluster species together in terms of personality structure similarity. The cluster analysis showed that Japanese and rhesus macaques were the most similar (see Figure 4). Assamese (grade 2), Tonkean (grade 4), and crested (grade 4) macaques were also similar. Barbary (grade 3) macaques clustered closer to the grade 2 and 4 species.

Goal 4: Sex Differences and Personality

We calculated fuzzy domain scores using the membership of items in each of the fuzzy personality set as weights. We tested whether sex differences in personality domain scores were related to social style by assessing the significance of a Sex × Social Style interaction in a mixed model controlling for age and troop differences. We hypothesized that females in less despotic social systems would be lower in Dominance-M and Aggressiveness-M (slope for females versus average < 0) and higher in Friendliness (slope for females versus average > 0). The results for Dominance-M ($\beta = .05$, 95% confidence interval [CI] = -.03, .11, $p = .21$) and Aggressiveness-M ($\beta = .00$, CI = -.07, .07, $p = .96$) were the opposite of our prediction (see Figure 5). The results for Friendliness-M matched our prediction ($\beta = .08$, CI = .01, .16, $p = .015$): females were rated as more friendly, compared with males, as social style went from despotic (grade 1) to egalitarian (grade 4).

During visualizations of our results we noticed considerable differences between males and females in personality score variance, so we also explored whether the amount of personality variance within each sex was related to social style (see Figure 6). We reasoned that the steepness of the female dominance hierarchy could restrict the expression of Dominance-M and Aggressiveness-M. Using a permutation test, we found that females in despotic, grade 1 species showed less variability in Dominance than males of these species (p = .004; after correcting for 12 tests p = .048). For species between grades 2-4, there was tendency for females to exhibit less variance in their Friendliness scores.

Discussion

Closely related species of macaques were similar in personality dimensions related to social affiliation but could be distinguished by the configuration of personality facets related to aggression and social dominance and these differences did not map crisply onto phylogenetic relatedness. Observer ratings of personality could be reduced to four dimensions in Japanese, Barbary, crested, and Tonkean macaques; and five dimensions in Assamese macaques. The most consistent findings were the presence a Friendliness dimension, across all of the macaque species we sampled and a separate Openness dimension in four out of five species. Interestingly, while the Openness dimension is common to a broad range of primates, including humans, Friendliness appears to be a personality dimension that is unique to macaques. Other aspects of personality structure differed among macaque species. Facets related to the great ape personality domains of Dominance and Neuroticism were also found in various configurations in all of the macaques sampled, but with different aspects being captured by the Dominance, Confidence, Anxiety, Irritability, and Opportunism dimensions. In support of our hypothesis that personality is related to social style, in examining how tightly bound lower-level personality facets were with each other, we found evidence for the formation of two distinct clusters: one cluster contained grade 1 species, whereas the other

cluster included the grades 2, 3, and 4 species. Specifically, Japanese macaques clustered with rhesus macaques and Assamese macaques clustered with Tonkean and crested macaques. Sex differences in social styles were capitulated in personality dimensions. Specifically, females in species with more relaxed social styles were rated as more friendly compared to conspecific males. Furthermore, in the highly despotic rhesus and Japanese macaques, females scores on Dominance-M facet derived from fuzzy set analysis showed significantly less variance than that of males, which could imply that females have fewer "degrees of freedom" (Butovskaya, 2004) for the expression of this personality trait.

Looking at commonalities across the items making up the domains in each species, we can define clusters of items that consistently describe lower-level facets or building blocks of personality, where the configuration of facets into domains is what differs between species. The Dominance-M facet described behavioral dispositions related to intervening decisively in social interactions and in taking actions without interference from others and was not strongly characterized by items related to aggression and intimidation. The personality facet capturing differences in social prowess appeared as part of the Dominance domain in rhesus, Japanese, and Tonkean macaques and as part of the Confidence domain in Barbary, crested, and Assamese macaques. Most of these domains also had a high positive loading from the item 'protective'. Aggressiveness, Irritability, and Opportunism, in contrast, either had a salient negative loading or a non-salient loading from this item. This is consistent with behavioral findings which show that socially dominant macaques tend to intervene on behalf of other individuals (Chapais, 2004).

Appearing as part of the Dominance domain in rhesus, Japanese, and Tonkean macaques and as a separate dimension in Barbary, crested, and Assamese macaques, behaviors relating to aggression were subsumed under the Aggressiveness-M facet. In addition to aggressive behaviors, this facet was supported by the membership of the items

'defiant,' 'irritable,' 'stingy/greedy,' and 'jealous.' This facet seems thus not only to capture aspects of aggression but also describes a behavioral pattern of individuals that run counter to the established dominance hierarchy and that the antagonism may be part of lashing out at others.

In contrast to the Dominance-M facet, which described how macaques act, the facets of Confidence-M and Anxiety-M seemed to capture how individuals react to different situations. Confidence-M, which appeared as its own dimension in rhesus but was combined with Dominance-M in other macaques, primarily described individuals' reactions in specific situations involving other animals. One of the items showing the greatest support, 'submissive,' describes whether an individual is likely to yield to others and thus the other items appear to describe the level of anxiety and distress that this yielding to others provokes. Only in rhesus macaques, however, did this facet vary independently from the Dominance-M facet. Anxiety-M likewise appeared as its own dimension in rhesus and Japanese macaques but was part of the Confidence dimensions of Barbary, crested, and Assamese macaques and Dominance in Tonkean macaques. Anxiety differed from Dominance-M and Confidence-M by not tying in specifically with behaviors related to the social order. This replicated the independence of the Confidence and Opportunism domains previously reported for Barbary macaques (Konečná et al., 2012). It was also revealing that the scores on macaque Dominance and Confidence dimensions correlated highly with scores on orangutan Intellect. Orangutan Intellect has been described as a blend of Openness and Conscientiousness (Weiss et al., 2006) but the macaque results suggest Intellect may be an ancestral facet related more to decisiveness and independence.

Friendliness was the dimension that was most uniquely characteristic of macaques when compared with apes. Friendliness-M contained a sub-facet similar to chimpanzee Agreeableness in only containing items related to the positive pole of the human trait that

(Weiss et al., 2011) dubbed altruism but was also characterized by a sociability sub-facet describing the Sociable–Solitary axis of behavior. Friendliness thus described a blended personality domain containing two facets that have become uncoupled in other species and its definition using behavioral adjectives is consistent across five different species of macaques. Tonkean macaques differed from the other species in having a second dimension, Sociability, which also described variation in affiliative behavior. This is similar to the split between Extraversion and Agreeableness seen in humans (Costa & McCrae, 1992), chimpanzees (King & Figueredo, 1997), gorillas (Gold & Maple, 1994), and orangutans (Weiss et al., 2006). Like chimpanzees and humans, Tonkean macaques have a high propensity to use affiliative contacts to reinforce bonds (De Marco, Cozzolino, Dessì-Fulgheri, & Thierry, 2011). The occurrence of intense, simultaneous affiliation behavior between multiple individuals (dubbed "collective arousal") in both species and the differentiation of multiple personality domains related to affiliative behavior may be explained by convergent coevolution.

Openness-M was supported by the membership of a consistent set of items across the macaque species sampled, and as Openness is also part of the personality architecture of chimpanzees (King & Figueredo, 1997) and humans, this is likely to be a general feature of primate personality (Freeman & Gosling, 2010), which would not appear to be directly related to social domains. Rather than it being an artifact of captivity, previous studies of rhesus macaque personality (Bolig et al., 1992; Capitanio, 1999; Stevenson-Hinde & Zunz, 1978) likely did not uncover this dimension because the questionnaires used did not probe items relevant to Openness. In support of this assertion, there was nothing that distinguished macaque Openness from the dimension as described in other species. For example, even though the item *playful* is part of chimpanzee Extraversion, it often has cross-loadings on to chimpanzee Openness (Weiss et al., 2009; Weiss et al., 2007). The lack of an independent

Openness domain in crested macaques, where this facet blended with Friendliness, might be a result of the smaller sample size in this species.

Although the precise phylogenetic relationships among rhesus, Japanese, and Assamese macaques remain somewhat in dispute, these species along with Tonkean and crested macaques are more closely related to each other than any of them are to Barbary macaques. As the only African member of the Macaque genus Barbary macaques are thought to be a sister clade to all Asian macaques and the best representative of the ancestral state of social behaviors for macaques (Thierry et al., 2000). If the collective personality structure of a species reflects its social structure and if it reflects an adaptive response to social selective pressures then we might expect Barbary macaque personality structure to be closest to the ancestral state. If this is the case then the ancestors of macaques would have differed from each other in terms of a combined Dominance/Confidence dimension related to social assertiveness, an Opportunism dimension defined by aggression and impulsivity, a Friendliness dimension capturing individual differences in social affiliation, and an Openness dimension related to curiosity and exploratory behavior. The appearance of separate Dominance and Anxiety dimensions in rhesus and Japanese macaques would then be derived characters. Conducting more comprehensive set of phylogenetic comparative analyses on personality traits, such as been done with attachment behavior in mammals (Fraley et al., 2005) and intelligence in primates (Reader, Hager, & Laland, 2011) will require personality data on enough species to achieve adequate power (Boettiger, Coop, & Ralph, 2012). Describing personality across all primate taxa would allow more thorough tests about evolutionary pathways of personality and the covariation of personality with social style. While macaques vary in terms of social style and social structure (Thierry et al., 2000) all macaques species have similar multi-male multi-female social organization (Melnick & Pearl, 1987) and life histories (Fooden, 1980). Thus other taxonomic comparisons will have to be

made to test other theories about the origins of animal personality differences, such as life-history explanations (Figueredo et al., 2006; Wolf, Sander van Doorn, Leimar, & Weissing, 2007), and understanding personality structure in terms the structure of environmental stimuli that individuals need to react to (Denissen & Penke, 2008).

Japanese and rhesus macaques, the two most closely related species, have the greatest resemblance in terms of their social patterns and highly strict dominance hierarchies (Thierry, 2000) and also share several aspects of their personality structure in common. In particular, both species exhibit separate Anxiety dimension and the fuzzy Aggressiveness-M facet was part of their Dominance dimension. This similarity was reflected when they were clustered in terms of the relative sizes of components made up of items from these fuzzy sets. Barbary, crested, and Assamese macaques, all species with more relaxed social styles, had a dimension (Irritability, Aggressiveness and Opportunism, respectively) that was independent of Confidence, and these species were likewise grouped together by the hierarchical clustering analysis. This separation in dimensions is similar to the division in long-tailed macaques, another grade 2 species, between Aggressive-Competitive and Assertive-Nonanxious personality domains (Uher et al., 2013). One possibility is that, given the relatively relaxed social style in these species, there is the opportunity for agonistic behaviors to vary independently from dominance and submissiveness (Konečná et al., 2012). This makes sense in light of the "degrees of freedom" individuals from these species enjoy in their social network (Butovskaya, 2004). However, Tonkean macaques lacked a separate dimension based on Aggressiveness-M even though they represent the opposite pole from rhesus macaques on the social structure scale. Alternatively, this dimension may not have been found in the Tonkean macaques because of the small sample size.

We had reasoned that if personality structure and social style are related, then sex differences in average personality scores would also be expected. While females in grade 1

societies show highly despotic behavior, when female social relationships are more egalitarian it could be the males who are more despotic (Schülke & Ostner, 2008). We found that females in species with more relaxed social styles were higher in Friendliness-M. We were also able to detect differences in personality variance: females in grade 1 species had significantly less variance in scores on Dominance-M, suggesting that their social strategies related to dominance positioning may be more restricted. Our results thus suggest that studying social style and sex differences using not just the mean level of behavioral expression, but also between- and within-individual variance, could be a fruitful line of research for primate personality. Doing so would require approaches to assessing personality that are more sensitive to the contextual expression of behavior (Uher, 2008), and that are less influenced by the potential effects of rater assumptions about sex differences (e.g., Sussman et al., 2013; Uher et al., 2013).

Completing the picture of how different behavioral facets start or stop covarying over evolutionary time (Araya-Ajoy & Dingemanse, 2014) will first require determining which macaque personality dimensions generalize to other populations of the same species. The Barbary macaques personality structure that we found was very similar to that found in an independent sample using a different personality questionnaire (Konečná et al., 2012) but multiple assessments of the other species should continue to be made as well (Sussman et al., 2013). Ecological factors may also influence the expression of individual behavioral tendencies as personality differences. For instance, while Japanese macaques are classified as more despotic, this label might only characterize the increased aggression in provisioned populations used in the foundational studies of this species (Hill, 1999). Japanese and rhesus macaque populations are also found in a wide range of climatic and ecological conditions. Further understanding will involve sampling closely and distantly related species that share

aspects of their social structure and populations within each species that differ in ecology and social dynamics (Chapman & Rothman, 2009).

Strong functional equivalences of adjective-derived personality dimensions across primate species have yet to be established (Uher, 2011). The analysis of personality dimensions as fuzzy sets can guide the development of models testing the structural equivalence of dimensions across species. Fuzzy set analysis can be used to pull out facets that are composed of related sets of items across species even when any particular facet is obscured within a species through correlation with other facets. The fuzzy set analysis also revealed that some items may be describing different features of separate personality dimensions (e.g., 'vulnerable' is descriptive of Confidence-M, Dominance-M, and Anxiety-M fuzzy sets). Nonhuman primate personality as assessed with the HPQ therefore does not appear to show simple structure, where each item loads on one and only one dimension. Human personality measures also do not show simple structure (Digman, 1990) and other ways of assessing nonhuman primate personality show similar cross-loadings between dimensions. Separating out the ‘meanings’ of HPQ items will require behavioral ratings that also incorporate the context of the behavior (Uher & Asendorpf, 2008) and behavior coding and testing approaches that assess specific behavioral units (Konečná et al., 2008; Sussman et al., 2013). This will serve as the basis for constructing personality taxonomies that start from individual items or behaviors, determining how they fit together as consistent facets, and discovering how these facets covary within a population or species to compose independent personality dimensions.

This comparative approach to personality dimensions also says something stronger about personality domains as evolutionary characters. These basic traits may be the result of opportunities for adaptive behavioral variation for meeting the social, ecological, and developmental challenges faced by big-brained, gregarious, and long-lived animals.

Simultaneously, the social style of a species or social structure of a population emerges from the interactions between and behavioral dispositions of the individuals making up each social unit. Factor models for each species are the first step in hypothesizing the building blocks constituting primate personality structures and determining how the variances within and covariances among personality facets are intertwined with social style. These scenarios will need to be contrasted with alternative explanations, including ecological circumstances such as feeding and mating competition that could drive species diversification in both social styles and personalities. While the identification of basic and blended personality dimensions using adjective ratings method may or may not provide the right answer, we believe it is asking the right question.

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Table 1

Sample sizes by macaque species, sex, and age groups and characteristics of ratings.

	Subjects			Age groups									
				Females				Males					
Species	Total	Female	Male	Infants	Juveniles	Adults[a]	Seniors	Infants	Juveniles	Adults[a]	Seniors	Raters	Raters/subject
Japanese	74	52	22	1	15	21	15	4	4	9	9	8	1-3 (M = 1.4)
Barbary	74	28	46	0	6	19	3	0	9	32	5	6	1-5 (M = 2.4)
Assamese	60	22	38	1	9	12	0	4	9	25	0	6	1-8 (M = 5.6)
Tonkean	46	22	24	0	2	14	6	0	8	9	7	9	3-9 (M = 4.0)
Crested	53	28	25	1	5	22	0	2	5	18	0	17	1-4 (M = 2.0)
Rhesus	125	73	52	23	14	23	13	25	5	13	9	---[b]	---

Note. Ages classified as infants (0-1 years old), juveniles (2-6 years old), sub-adults or adults (7-14 years old), or senior adults (ages 15+). *M* = mean.

[a] Adult age category includes adults and sub-adults.

[b] Personality scores for rhesus macaques were mean scores from a previous study.

Table 2

Item reliabilities summary.

	ICC(3, 1)		*ICC*(3, *k*)	
Species	mean	range	mean	range
Japanese	.40	-.15, .79	.47	-.22, .85
Barbary	.30	-.01, .68	.48	-.01, .83
Assamese	.22	.05, .61	.57	-.23, .61
Tonkean	.36	-.01, .68	.65	-.03, .89
Crested	.37	-.18, .71	.51	-.46, .83

Note. Intraclass correlation coefficients (ICC) of the item rating from 1 rater or the mean of *k* raters.

Table 3

Macaque personality dimensions.

Species (grade)		Example items
Japanese (1)	Dominance	+dominant, +submissive, +aggressive
	Openness	+innovative, +inventive, +curious
	Friendliness	+gentle, +affectionate, +friendly
	Anxiety	+disorganized, +unperceptive, +erratic
Barbary (3)	Confidence	-vulnerable, -timid, -anxious
	Openness	+imitative, +disorganized, +innovative
	Friendliness	+active, +sociable, +affectionate
	Irritability	-gentle, -friendly, irritable
Assamese (2)	Confidence	-dependent, -anxious, -vulnerable
	Activity	-lazy, -stable, - unemotional
	Openness	+thoughtless, -conventional, +innovative
	Friendliness	+helpful, +affectionate, +sympathetic
	Opportunism	+jealous, +stingy, +bullying
Tonkean (4)	Dominance	+stingy, +persistent, -vulnerable
	Openness	+active, -lazy, +playful
	Friendliness	+helpful, +sympathetic, +sensitive
	Sociability	-solitary, +friendly, +depressed
Crested (4)	Friendliness	+sympathetic, +friendly, +affectionate
	Confidence	-fearful, +dominant, -vulnerable
	Aggressiveness	+erratic, -gentle, +reckless
	Excitability	-unemotional, +decisive, +manipulative
Rhesus (1)	Confidence	-fearful, -submissive, -timid
	Openness	+inquisitive, +thoughtless, +innovative
	Dominance	+bullying, +stingy, +aggressive
	Friendliness	+helpful, +friendly, +affectionate
	Activity	-conventional, -predictable, -lazy
	Anxiety	-cool, +quiting, +anxious

Note. Dimensions for each species are sorted by eigenvalue and each domain is described with its three characteristic items. Plus and minus signs before each item indicate positive or negative loading on the dimension. See Supplementary Material for full descriptions.

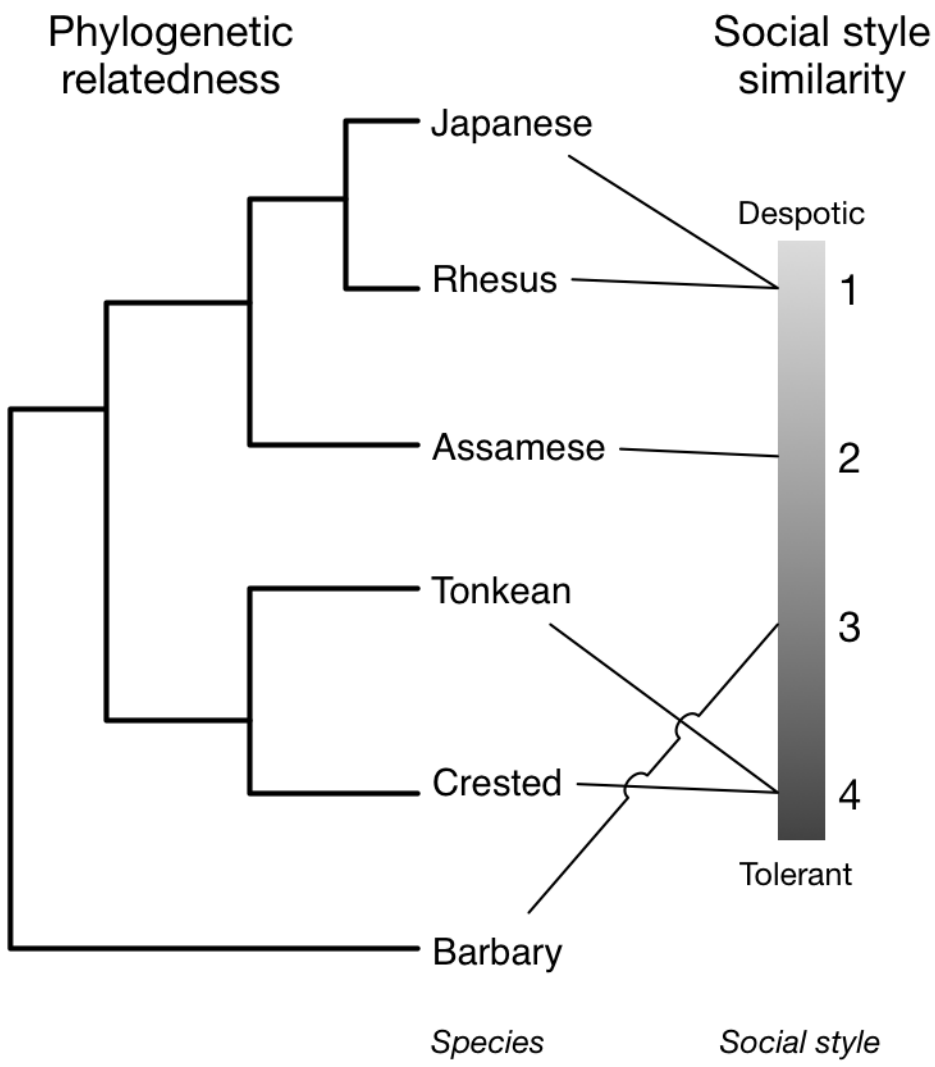

Figure 1. Cladogram of relationships between macaques species used in this study compared to social style gradient (1 = despotic, 4 = tolerant). Figure by the authors, licensed under a Creative Commons Attribution 4.0 License and published under the terms of this license.

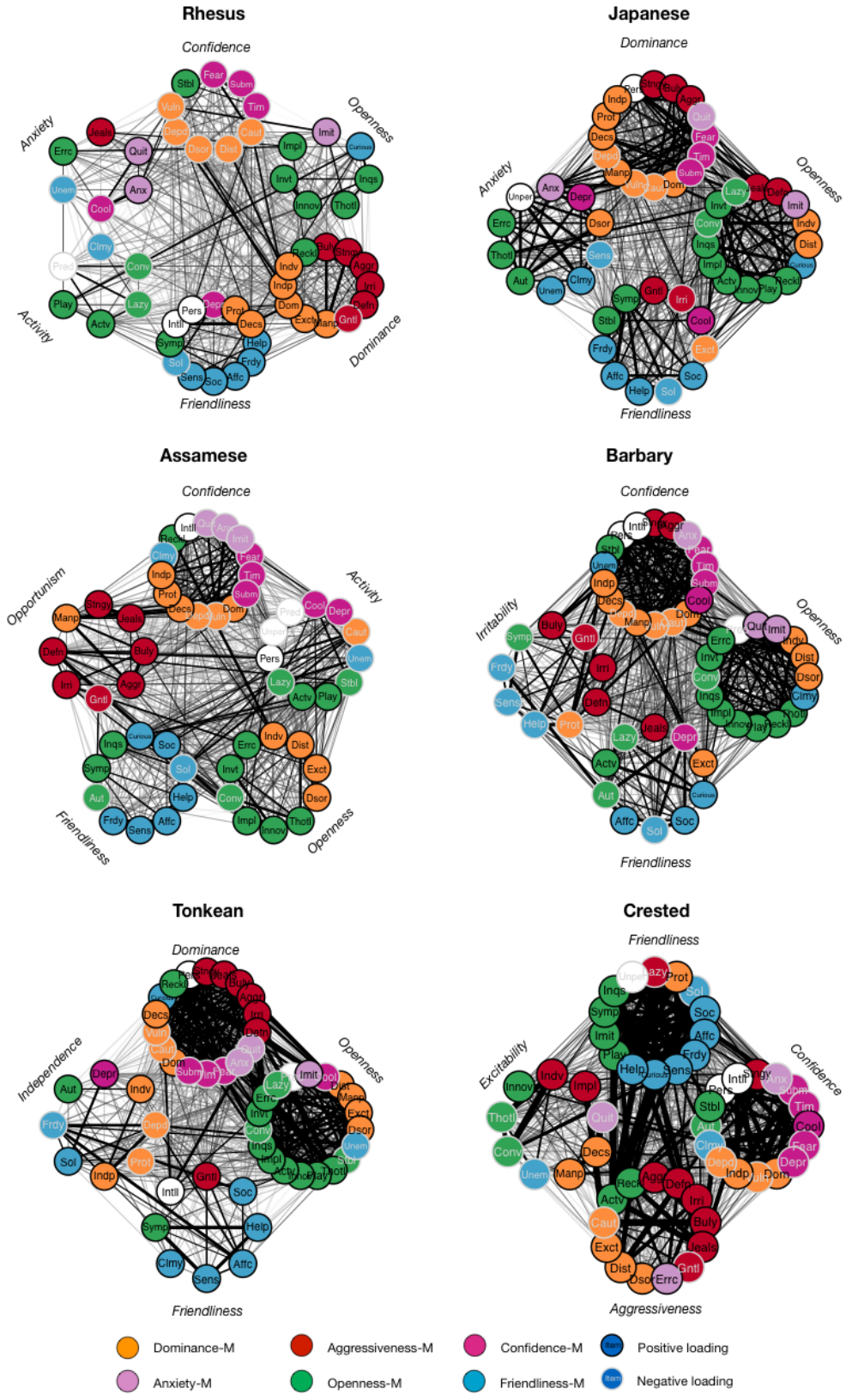

Figure 2. Graphs of personality structures. Personality items (circles labelled with item abbreviation, black text = positive loading, gray text = negative loading) are organized

grouped by personality dimensions (italics). Lines between personality items indicate strength of correlation. Items colored by the fuzzy set that the item has the greatest membership in. Items with a white background did not have salient membership in any fuzzy sets. Personality item abbreviations are listed in the supplementary material. Figure created in qgraph by the authors, licensed under a Creative Commons Attribution 4.0 License and published under the terms of this license.

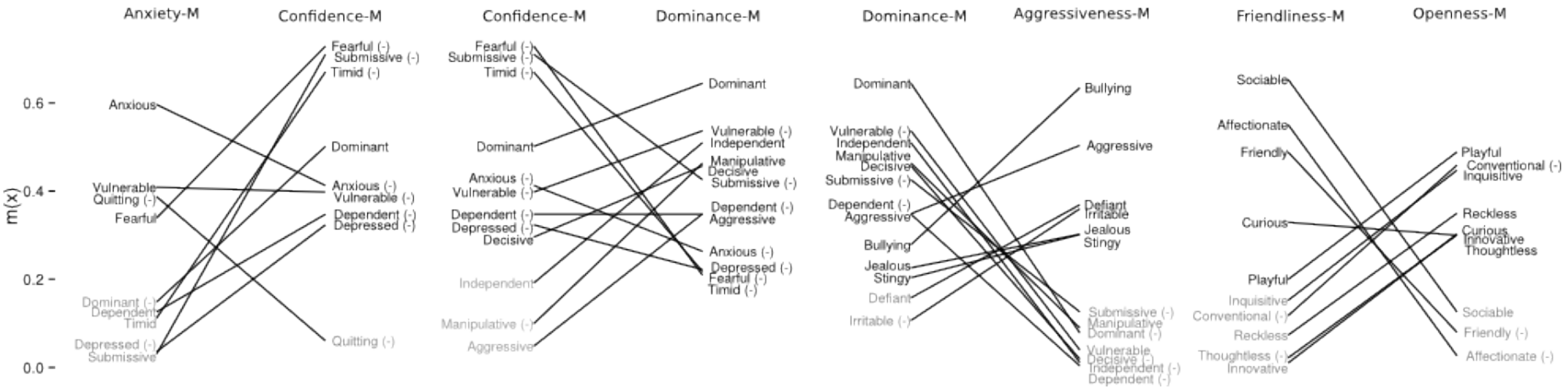

Figure 3. Comparison of item membership between fuzzy sets. Greater degrees of membership show the items that uniquely define each fuzzy personality dimension across species. m(x) = membership in the fuzzy set, or the absolute value of the minimum factor loadings from the personality dimensions composing each fuzzy set. Only items with m(x) >= 0.3 in one of the fuzzy sets being compared are plotted. "(-)" after the item name indicate a negative loading. Figure by the authors, licensed under a Creative Commons Attribution 4.0 License and published under the terms of this license.

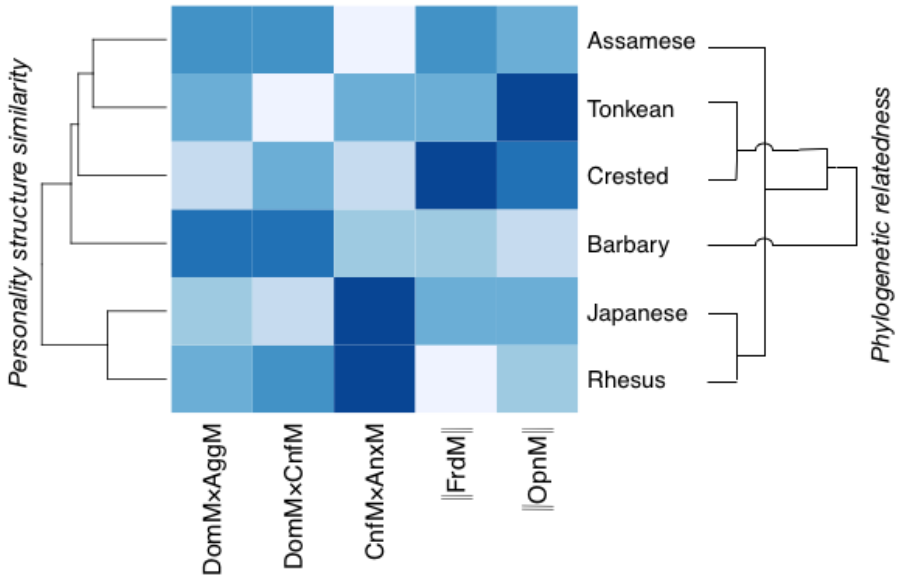

Figure 4. Species clustered by similarity of personality structure compared against phylogenetic relatedness. Species were ranked on five measures of personality structure (labelled on the bottom), then ranked. Number of differences in rank ('Manhattan' distance) was calculated between each species and then used to cluster them (left branching tree) showing that Japanese macaques are most similar to rhesus macaques and Assamese macaques most similar to Tonkean macaques, using these metrics. For fuzzy sets X and Y, X×Y is a calculation of the independence of X and Y within the species and ||X|| is the size of dimension composed of salient items from X. DomM = Dominance-M, CnfM = Confidence-M, AnxM = Anxiety-M, FrdM = Friendliness-M, OpnM = Openness-M. Figure by the authors, licensed under a Creative Commons Attribution 4.0 License and published under the terms of this license.

Figure 5. Sex differences in personality scores across social style grades (rhesus, Japanese = 1; Assamese = 2; Barbary =3, Crested = 4, Tonkean = 4). Figure by the authors, licensed under a Creative Commons Attribution 4.0 License and published under the terms of this license.

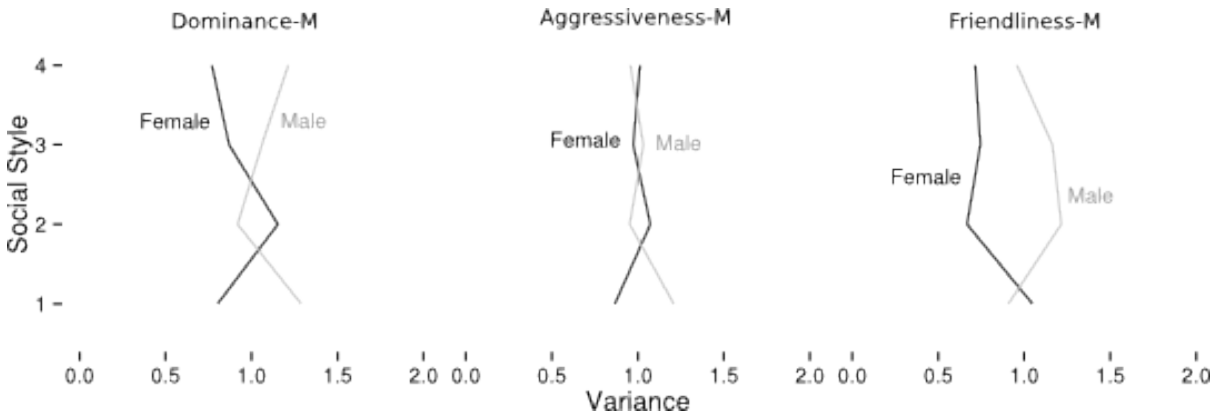

Figure 6. Sex differences in variance of personality scores across social style grades (rhesus, Japanese = 1; Assamese = 2; Barbary =3, Tonkean = 4). Figure by the authors, licensed under a Creative Commons Attribution 4.0 License and published under the terms of this license.

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Supplementary Material

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Derivation of Hominoid Personality Questionnaire items

Forty-one of the Chimpanzee Personality Questionnaire adjectives were taken from the Big Five subscales (Goldberg, 1990) with descriptive sentences and two additional items, 'clumsy' and 'autistic', added by King and Figueredo (1997). Because a previous study of chimpanzees found that Neuroticism and Openness did not replicate in a different habitat, Weiss, King, and Perkins (2006) added three items that would potentially describe Neuroticism ('anxious', 'cool', and 'vulnerable') and two that could flesh out Openness ('conventional' and 'curious'). Together these 48 items comprised the Orangutan Personality Questionnaire (OPQ). In another study of chimpanzees, Weiss et al. (2009) added additional items, again derived from the human literature (McCrae & Costa, 1985), to assess Conscientiousness ('distractible', 'quitting', and 'thoughtless') and Openness ('individualistic' and 'innovative'). The HPQ was later modified by Weiss, Adams, Widdig, and Gerald (2011) for use in assessing free-ranging and/or wild monkeys, which involved replacing references in the adjective descriptions to "enclosure" with the word "environment". An electronic version of the HPQ can be obtained from `http://extras.springer.com/2011/978-1-4614-0175-9/`

Item reliabilities

Table S1: Intraclass correlation coefficients for personality items.

	Japanese		Barbary		Assamese		Tonkean		Crested	
ICC	3,1	3, *k*	3,1	3, *k*	3,1	3, *k*	3,1	3, *k*	3,1	3, *k*
Fearful	.61	.69	.25	.65	.47	.68	.51	.81	.28	.45
Dominant	.66	.73	.58	.88	.57	.76	.67	.89	.59	.74
Persistent	.41	.49	.12	.43	.38	.59	.34	.67	.41	.59
Cautious	.45	.53	.24	.64	.22	.40	.45	.76	.08	.15
Stable	.44	.53	.20	.58	.43	.65	.32	.65	.19	.33
Autistic	.50	.58	.05	.23	.65	.81	.46	.77	.56	.72
Curious	.32	.40	.31	.72	.25	.45	.26	.59	.37	.54
Thoughtless	.42	.51	.10	.38	.32	.53	.34	.67	.32	.48
Stingy/greedy	.52	.60	.19	.56	.10	.22	.57	.84	.52	.69
Jealous	.38	.47	.13	.46	.16	.31	.33	.67	.25	.40
Individualistic	.05	.06	.12	.43	.29	.49	.23	.54	.50	.67
Reckless	.62	.69	.09	.35	.19	.36	.46	.77	.44	.61
Sociable	.21	.27	.29	.70	.50	.71	.46	.77	.66	.80
Distractable	.11	.14	.09	.35	.20	.37	.01	.04	.25	.41
Timid	.61	.69	.39	.78	.41	.62	.48	.79	.51	.68
Sympathetic	.32	.40	.05	.24	.22	.40	.33	.66	.57	.73
Playful	.72	.78	.61	.90	.68	.83	.68	.89	.71	.83
Solitary	.64	.71	.45	.82	.48	.69	.36	.69	.67	.80
Vulnerable	.47	.56	.41	.79	.47	.68	.60	.85	.55	.72
Innovative	.42	.50	.05	.24	.17	.33	.44	.76	.28	.44
Active	.80	.85	.38	.78	.43	.64	.51	.81	.58	.74
Helpful	.53	.62	.18	.56	.30	.50	.31	.64	.31	.48
Bullying	.54	.62	.25	.65	.23	.42	.61	.86	.28	.45
Aggressive	.53	.62	.27	.68	.18	.34	.54	.83	.39	.57
Manipulative	.49	.58	.23	.63	.22	.40	.22	.53	.21	.35
Gentle	.22	.28	.17	.54	.10	.21	.28	.61	.25	.40
Affectionate	.43	.52	.16	.51	.22	.41	.32	.65	.55	.71
Excitable	.10	.13	.22	.61	.30	.51	.31	.64	.11	.20
Impulsive	.12	.16	.21	.60	.13	.27	.32	.66	.20	.33
Inquisitive	.29	.36	.33	.74	.27	.47	.35	.68	.39	.57

Submissive	.63	.70	.51	.85	.40	.61	.60	.86	.57	.73
Cool	.08	.11	.14	.48	.22	.41	.25	.57	.33	.50
Dependent/ follower	.07	.09	.42	.80	.31	.51	.51	.80	.07	.13
Irritable	.41	.50	.19	.56	.36	.57	.36	.70	.32	.49
Unperceptive	.41	.49	.14	.47	−.01	−.01	−.01	−.03	.18	.31
Predictable	−.08	−.12	.08	.33	.24	.43	.28	.61	.01	.01
Decisive	.43	.51	.32	.73	.26	.45	.31	.64	.45	.63
Depressed	.34	.42	.24	.64	.36	.57	.44	.76	.22	.36
Conventional	.32	.39	.12	.43	.09	.20	.33	.66	.59	.74
Sensitive	.30	.38	.09	.37	.10	.21	.11	.33	.51	.68
Defiant	.77	.82	.15	.49	.07	.16	.34	.67	.33	.50
Intelligent	−.15	−.22	.22	.61	.24	.43	.35	.68	.38	.56
Protective	.65	.72	.36	.76	.44	.65	.26	.58	.59	.75
Quitting	.37	.46	.11	.40	.23	.42	.07	.22	.06	.11
Inventive	.22	.28	.08	.33	.25	.45	.28	.61	−.18	−.46
Clumsy	.49	.57	.13	.46	.30	.51	.41	.74	.32	.49
Erratic	.45	.54	.08	.32	.22	.40	.20	.50	.20	.33
Friendly	.22	.29	.10	.38	.36	.57	.51	.81	.51	.68
Anxious	.57	.65	.23	.63	.32	.53	.33	.67	.42	.60
Lazy	.31	.39	.33	.74	.44	.65	.42	.75	.43	.61
Disorganized	.25	.32	.16	.52	.36	.57	.10	.30	.29	.45
Unemotional	.55	.63	.19	.57	.30	.50	.44	.76	.35	.53
Imitative	.51	.59	.22	.61	.44	.66	.10	.31	.71	.83
Independent	.43	.51	.27	.68	.12	.25	.47	.78	.42	.59

Data reduction

Table S2: Intercorrelations for components derived via promax rotation. Act = activity, Anx = anxiety, Cnf = confidence, Exc = Excitability, Frd = Friendliness, Opn = openness, Opp = opportunism.

Japanese macaque

	Dom	Opn	Frd
Opn	.26		
Frd	−.09	−.09	
Anx	.13	.17	−.30

Barbary macaque

	Cnf	Opn	Frd
Opn	−.26		
Frd	.07	.43	
Opp	−.18	.29	.14

Assamese macaque

	Cnf	Act	Opn	Frd
Act	.01			
Opn	−.00	.28		
Frd	.07	.21	−.11	
Opp	.24	.17	.27	−.08

Tonkean macaque

	Dom	Opn	Frd
Opn	.24		
Frd	.32	.00	
Ind	.06	.23	.01

Crested macaque

	Frd	DomAgg
Dom	−.28	
Agg	−.20	.26
Exc	.01	.24

Personality component descriptions

Japanese macaques *(Macaca fuscata)*

Parallel analysis suggested a five-component solution (eigenvalues 13.3, 9.1, 7.2, 3.7, and 2.6). However, the adjusted eigenvalue of the last component retained was 1.01, indicating it was only marginally above what would be expected by chance. An examination of the scree plot showed that the fifth component had an eigenvalue that did not differ substantially from that of the sixth component. We therefore extracted four components to describe Japanese macaque personality (see Table 1).

The first component was positively defined by items such as *dominant* and *aggressive* and negatively by items such as *submissive* and *fearful*. These items describe traits related to both Machiavellianism and social potency (Maestripieri, 2007), which in humans are found in the negative pole of Agreeableness (Goldberg, 1990), and to reactions within the social environment, similar to human Neuroticism. High-scoring individuals would thus be competent in social interactions and confident when facing challenges within their environment. Low-scoring individuals would be more cautious when confronting such challenges and would readily yield during conflicts. This dimension was similar to the confidence–fearful dimension in rhesus macaques (Stevenson-Hinde & Zunz, 1978). Unit-weighted scores on this domain (Table 5) were correlated with the rhesus macaque dimensions of Confidence and Dominance and were almost identical to the chimpanzee dimension Dominance. We therefore named this component 'Dominance'.

The second component was defined by items related to exploratory behavior, such as *curious*, which in humans makes up Openness (McCrae & Costa, 1985). It also contained items related to low Conscientiousness and high Neuroticism in humans, such as *impulsive* (Costa & McCrae, 1992; Goldberg, 1990). Individuals scoring high on this dimension would be highly exploratory and also prone to act impulsively. Low scorers would in contrast be less active and playful in their environment. This dimension resembled the Openness dimension in rhesus macaques (Weiss et al., 2011) so we named this component 'Openness'.

The third component was related to social affiliation, including items such as *social* and *solitary*, and to cooperative behavior, with items like *gentle* and *helpful*. It was thus similar to facets of human Extraversion and Agreeableness (Goldberg, 1990). It also contained items (*irritable*, *excitable*, and *stable*), related to high and low human Neuroticism (Costa & McCrae, 1992). High scorers would therefore seek out social contact and would act

cooperatively in social situations. Low scorers, meanwhile, would shun social engagement. This dimension was extremely similar to Friendliness in rhesus macaques (Weiss et al., 2011) and was similar in resembling chimpanzee Extraversion and Agreeableness and orangutan Agreeableness (Table 5). We named this component 'Friendliness'.

The final component contained items such as *erratic* and *disorganized* that were related to human Conscientiousness (Goldberg, 1990). It also contained items related to high Neuroticism in humans, such as *anxious* and *depressed* (Costa & McCrae, 1992). High scorers would therefore be volatile in their behavior and tense while low scorers would be less emotional. This dimension differed from the first component, Dominance, in that it seems to describe reactions to less context-specific stressors, similar to the Anxiety/Confidence division seen in rhesus macaques (Weiss et al., 2011). We named this domain 'Anxiety'.

Because of the results of the parallel analysis, we also tried a five-component solution. We calculated factor congruence coefficients using the psych package in R (Revelle, 2011) and found that the four dimensions were also well described in the five-component solution (congruence coefficients = .90–1.0). The highest loading on the fifth component was (not) *cool* (-.69) and the component also contained the items *excitable*, *reckless*, *impulsive*, and (not) *stable*. This component had factor congruences of .46 and -.58 with Openness and Friendliness from the four-component solution and had several salient cross-loadings on the other components. While it resembled rhesus macaque Excitability (Stevenson-Hinde & Zunz, 1978) it did not represent a clear separate dimension in Japanese macaques. We therefore retained the four-component solution.

Table S2: Japanese macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings (≥|.40|) are bolded. Dom = Dominance, Opn = Openness, Frd = Friendliness, Anx = Anxiety. h^2 = communalities.

	Dom	Opn	Frd	Anx	h^2
Dominant	**.93**	.02	.02	−.21	.90
Submissive	**−.89**	.08	−.13	−.09	.82
Timid	**−.87**	.03	−.06	.11	.77
Aggressive	**.86**	.17	−.20	.10	.81
Bullying	**.81**	.27	−.24	.06	.79
Fearful	**−.81**	.17	−.11	.34	.80
Manipulative	**.63**	.11	.14	−.27	.51
Independent	**.63**	.23	−.28	.29	.61
Persistent	**.61**	**.47**	.00	.06	.60
Stingy/greedy	**.61**	.26	−.10	.32	.55
Decisive	**.60**	.33	.25	−.09	.54
Cautious	**−.60**	−.17	.10	.21	.44
Vulnerable	**−.55**	.06	−.23	**.41**	.53
Dependent/follower	**−.53**	**.46**	.15	.13	.53
Quitting	**−.44**	−.19	−.30	**.43**	.50
Protective	**.44**	.09	**.43**	.16	.41
Innovative	.06	**.78**	.08	−.05	.62
Inventive	.06	**.77**	.25	−.11	.67
Curious	.19	**.76**	.33	−.10	.74
Playful	−.19	**.75**	.20	−.06	.64
Inquisitive	.05	**.72**	.29	.04	.61
Active	.20	**.70**	.13	.12	.56
Impulsive	.26	**.64**	**−.42**	−.07	.66
Imitative	−.03	**.63**	.35	.38	.67
Reckless	**.40**	**.60**	−.27	−.07	.59
Jealous	**.55**	**.57**	.02	.03	.63
Defiant	.39	**.56**	−.26	.29	.62
Distractable	−.37	**.49**	−.08	.05	.39
Individualistic	.04	**.47**	−.30	.22	.36
Conventional	−.04	**−.46**	.14	−.21	.27
Gentle	−.25	−.01	**.81**	−.09	.73
Affectionate	.03	.30	**.80**	−.15	.75
Sympathetic	.03	.31	**.71**	−.22	.65
Friendly	−.16	**.49**	**.69**	−.17	.77
Irritable	.36	.11	**−.69**	.00	.62
Sociable	.31	.37	**.65**	−.13	.68
Excitable	.13	**.44**	**−.60**	.04	.57
Solitary	−.19	−.09	**−.57**	.29	.45
Helpful	.22	.34	**.56**	−.09	.49
Stable	.26	−.30	**.50**	−.31	.50

Disorganized	−.31	.07	−.05	**.79**	.72
Unperceptive	−.01	−.01	−.11	**.76**	.59
Erratic	.03	.31	−.14	**.76**	.69
Clumsy	−.01	−.12	−.10	**.74**	.58
Autistic	−.20	.20	−.09	**.74**	.64
Depressed	−.32	−.02	−.32	**.70**	.70
Unemotional	.10	−.21	.40	**.68**	.68
Anxious	**−.56**	.09	−.20	**.67**	.82
Sensitive	−.19	−.01	.14	**−.60**	.42
Thoughtless	.32	**.42**	−.02	**.45**	.49
Lazy	−.32	−.38	−.20	.05	.29
Cool	.37	−.20	.38	−.02	.32

Barbary macaques *(Macaca sylvanus)*

Parallel analysis suggested four components (eigenvalues 15.7, 10.6, 5.0, 4.2) which was supported by an examination of the scree plot. Item loadings are listed in Table 2. The first component was large and encompassing and explained 38% of the variance in item scores. It was primarily characterized by items (*vulnerable, timid*, and *fearful*) related to human Neuroticism as well as negative (*dominant*) pole of human Agreeableness (Goldberg, 1990). This dimension also resembled human Conscientiousness by loading on items such as *persistent* and *decisive*. Individuals who score high on this trait would therefore be commanding in a variety of situations while low-scorers would be more cautious and timid. This component was very similar to the Confidence dimension found in a previous study of Barbary macaques (Konečná, Weiss, Lhota, & Wallner, 2012) though it contained other items (*manipulative, stingy*) that in the other study composed a separate Opportunism dimension. Unit-weighted domain scores correlated positively with scores on rhesus macaque Dominance, Confidence, and Friendliness (Table 5). This component also strongly resembled orangutan Neuroticism (reversed). However, while this component had a high loading from the item *dominant*, it did not resemble rhesus macaque Dominance in that it did not have many items related to aggressive behavior, which instead loaded on the fourth component. We therefore named this component 'Confidence'.

The second component was characterized primarily by positive loadings on items related to human Openness to Experience (McCrae & Costa, 1985), such as *innovative* and *imitative*. High scorers would therefore be high on exploratory behavior. Domain scores revealed this component to be similar to rhesus macaque and chimpanzee Openness but it shared some features with rhesus macaque Activity and chimpanzee and orangutan Extraversion (see Table 5). In terms of item content, it was similar to the Activity/Excitability domain found previously in Barbary macaques. We named it 'Openness'.

The third component was similar to human Agreeableness (items like *gentle* and *affectionate*) and to human Extraversion (*sociable*, not *solitary*, *active*). High scorers would seek out social affiliation while low scorers would be more solitary. It thus resembled the Sociable-Solitary and Friendliness domains in rhesus macaques, particularly in being a blend of Extraversion- and Agreeableness-like features. However, this component differed from the Friendliness domain previously described in Barbary macaques (Konečná et al., 2012) in that it did not contain items related to the negative pole of Agreeableness (*aggressive, bullying*). We named this component 'Friendliness'.

142 The fourth component was composed of items related to the positive (*gentle*,
143 *sympathetic, protective*) and negative (*bullying*) poles of Agreeableness and the positive pole
144 of Neuroticism (*irritable*) in humans (Goldberg, 1990). It also had high cross-loadings with
145 the first component on items related to aggression. Individuals high on this dimension would
146 be aggressive toward conspecifics. Low scorers would be constrained and supportive in
147 social relations. The items in this component resembled rhesus macaque, chimpanzee, and
148 orangutan Dominance (Table 5). The item content and correlations with scores on the rhesus
149 structure was similar to a dimension in Barbary macaques that had been previously identified
150 as Friendliness (Konečná et al., 2012) in that both had correlations with rhesus Dominance
151 and Friendliness scores with opposite signs. However, the currently described dimension did
152 not have loadings on other items that mark the Extraversion-like aspects of rhesus
153 Friendliness such as *sociable* and *solitary.* Because this component related to forceful
154 behavior but without the controlled Machiavellianism of Dominance or Confidence (in that it
155 did not load saliently on items like *manipulative*), we named it ‘Irritability'.
156

Table S3: Barbary macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings (≥|.40|) are bolded. Cnf = Confidence, Irr = Irritability , Frd = Friendliness, Opn = Openness. h^2 = communalities.

	Cnf	Opn	Frd	Irr	h^2
Vulnerable	**-0.90**	0.08	-0.10	0.08	0.83
Timid	**-0.88**	0.03	-0.17	0.03	0.80
Fearful	**-0.88**	0.10	-0.05	0.11	0.79
Dominant	**0.84**	-0.36	0.13	-0.08	0.85
Anxious	**-0.83**	0.15	-0.10	0.15	0.75
Persistent	**0.82**	-0.05	0.21	-0.06	0.72
Submissive	**-0.75**	0.33	0.02	-0.13	0.69
Dependent	**-0.73**	0.16	**0.45**	0.00	0.75
Independent	**0.72**	-0.06	-0.26	0.07	0.60
Aggressive	**0.71**	0.08	0.19	**0.50**	0.80
Stable	**0.70**	-0.30	0.03	-0.44	0.76
Cautious	**-0.69**	-0.27	-0.39	-0.03	0.71
Cool	**0.67**	-0.22	-0.05	-0.36	0.63
Decisive	**0.67**	**-0.50**	0.02	-0.02	0.70
Intelligent	**0.67**	-0.30	0.08	-0.36	0.67
Stingy	**0.63**	0.16	0.13	0.30	0.53
Manipulative	**0.63**	0.08	0.33	0.09	0.52
Unemotional	**0.53**	0.01	-0.31	-0.16	0.40
Imitative	-0.16	**0.82**	0.19	-0.12	0.75
Disorganized	-0.32	**0.82**	0.09	0.01	0.78
Innovative	0.12	**0.81**	0.01	-0.03	0.67
Reckless	0.11	**0.77**	0.22	0.27	0.73
Inventive	0.17	**0.75**	-0.07	-0.16	0.61
Quitting	-0.40	**0.73**	0.24	0.11	0.76
Clumsy	-0.37	**0.72**	-0.14	0.12	0.69
Playful	0.00	**0.67**	0.46	-0.32	0.76
Distractable	-0.59	**0.64**	0.23	0.01	0.81
Thoughtless	-0.29	**0.62**	0.35	0.19	0.63
Predictable	0.09	**-0.62**	**-0.44**	-0.11	0.60
Impulsive	-0.19	**0.62**	0.42	0.32	0.70
Conventional	0.06	**-0.56**	-0.28	-0.26	0.46
Erratic	-0.38	**0.54**	0.07	0.24	0.51
Inquisitive	-0.16	**0.53**	0.41	-0.21	0.53
Individualistic	0.13	**0.50**	0.03	0.31	0.36
Active	0.00	0.28	**0.78**	-0.05	0.69
Sociable	**0.44**	0.13	**0.70**	-0.37	0.84
Lazy	-0.04	-0.21	**-0.69**	0.09	0.53
Depressed	**-0.44**	0.02	**-0.68**	0.06	0.66
Solitary	-0.46	-0.19	**-0.67**	0.24	0.75
Curious	-0.20	0.30	**0.66**	-0.02	0.57
Jealous	0.23	0.20	**0.61**	**0.41**	0.62
Excitable	**-0.46**	0.17	**0.57**	0.38	0.71

Affectionate	0.13	0.17	**0.55**	**−0.55**	0.65
Autistic	−0.38	0.10	**−0.51**	−0.03	0.41
Gentle	−0.26	−0.09	0.00	**−0.81**	0.73
Friendly	0.01	0.14	**0.49**	**−0.74**	0.80
Irritable	−0.11	−0.17	0.08	**0.71**	0.55
Sympathetic	0.21	−0.26	−0.04	**−0.70**	0.60
Sensitive	0.12	−0.12	0.16	**−0.63**	0.46
Bullying	**0.60**	0.06	0.20	**0.63**	0.81
Protective	**0.52**	−0.27	0.11	**−0.62**	0.74
Helpful	**0.48**	−0.08	0.27	**−0.56**	0.62
Defiant	0.33	0.30	0.28	**0.37**	0.42

160

Assamese macaques *(Macaca assamensis)*

Parallel analysis suggested that five components be retained (eigenvalues = 14.0, 10.4, 5.6, 3.7, and 3.4) which agreed with an examination of the scree plot. Item loadings for the Assamese macaque structure are listed in Table 3.

After reflecting the first component (i.e., multiplying its loadings by -1), it was chiefly defined by items related to human Neuroticism (Goldberg, 1990), such as negative loadings on *anxious* and *vulnerable* and positive loadings on *independent*. It also had positive loadings on the items *decisive* and *intelligent* and negative loadings on the items *quitting* and *reckless* related to human Conscientiousness. The loadings on *dominant* and *submissive* also suggested human agreeableness. Monkeys scoring high on this domain could therefore be described as competent in meeting challenges in their environment. Individuals scoring low on this component would display anxiety across a variety of situations. Items making up this component were similar in nature to the Confidence dimensions in rhesus macaques. Domain scores from unit-weighted loadings correlated positively with rhesus macaque Dominance and Confidence and negatively with anxiety (see Table 5). It was also highly similar to chimpanzee and orangutan Dominance. However, like with the Barbary macaques, this component was not strongly characterized by items related to the negative pole of human Agreeableness. We therefore named this component 'Confidence'.

After reflecting the second component, it had negative loadings from items related to human Neuroticism (*stable*, *unemotional*) and to human conscientiousness (*lazy*, *persistent*). It was also defined positively by two items, *active* and *playful*, related to Extraversion in humans. High scorers would therefore be active but stable when engaging with their environment while low scorers would be more cautious and less energetic. This component was similar to Activity in rhesus macaques. Domain scores also highly resembled scores on orangutan extraversion. Given its similarity to the rhesus macaque domains, we named this component 'Activity'.

The third component had items, such as *innovative* and *inventive*, related to the positive pole of human Openness to Experience (Costa & McCrae, 1992). It also had negative markers of human Conscientiousness, such as *distractible* and *disorganized*. High scorers would thus be novel yet erratic in their behavior whereas low scorers might be more typical. This domain was therefore similar to both rhesus macaque Openness and Activity. The domain scores also revealed that it was similar to Anxiety in rhesus macaques and was

positively correlated with domain scores on chimpanzee Neuroticism and Openness and negatively with chimpanzee Conscientiousness. We named this component 'Openness'.

The fourth component showed the same blend of Agreeableness- (*helpful*, *affectionate*) and Extraversion-like items (*sociable*, (not) *solitary*) as Friendliness found previously in rhesus and Barbary macaques. Domain scores correlated positively with rhesus macaque Friendliness, Openness, and Activity and with chimpanzee and orangutan Extraversion and Agreeableness (Table 5). We therefore named this component 'Friendliness'.

The last component was defined by items, such as *stingy/greedy*, *bullying*, and *irritable*, that characterize the negative pole of human Agreeableness. It was similar in content to the Barbary macaque Opportunism dimension and likewise correlated positively with domain scores on rhesus, chimpanzee, and orangutan Dominance and negatively with chimpanzee Conscientiousness (Table 5). We therefore labeled this component 'Opportunism'.

Table S4: Assamese macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings (≥|.40|) are bolded. Cnf = Confidence, Act = Activity, Opn = Openness, Frd = Friendliness, Opp = Opportunism. h^2 = communalities.

	Cnf	Act	Opn	Frd	Opp	h^2
Dependent/follower	**-.86**	.15	-.15	.10	-.23	.84
Anxious	**-.85**	-.31	.12	-.06	.07	.85
Vulnerable	**-.82**	-.21	.05	-.09	-.20	.76
Fearful	**-.80**	.09	.07	.03	-.02	.66
Timid	**-.80**	-.23	.03	-.05	-.15	.72
Submissive	**-.80**	-.02	-.01	.06	-.36	.76
Dominant	**.77**	-.06	.08	-.01	**.51**	.86
Independent	**.74**	-.22	.21	-.21	.05	.68
Decisive	**.73**	-.12	.19	.08	.37	.72
Protective	**.71**	-.25	-.06	**.41**	.22	.79
Quitting	**-.64**	-.37	.08	-.19	.06	.59
Clumsy	**-.59**	-.26	.36	.30	.04	.64
Intelligent	**.59**	.07	.02	**.44**	.13	.57
Reckless	**-.58**	-.17	**.56**	-.16	-.17	.73
Lazy	.09	**-.84**	-.16	-.26	.09	.81
Stable	.06	**-.77**	-.23	.06	**-.45**	.85
Unemotional	.06	**-.76**	-.33	-.09	-.16	.72
Depressed	-.41	**-.72**	.07	-.36	-.10	.83
Cool	.35	**-.66**	-.11	.00	-.18	.60

Predictable	−.21	**−.62**	−.15	.27	.08	.53
Active	−.20	**.62**	**.48**	.34	−.11	.79
Playful	−.27	**.56**	**.49**	.40	−.18	.81
Cautious	−.30	**−.53**	−.29	−.27	−.03	.53
Persistent	**.45**	**−.46**	**.43**	.18	.28	.71
Unperceptive	−.33	−.35	.33	−.15	−.10	.37
Thoughtless	.01	.09	**.79**	.03	.08	.64
Conventional	−.11	−.36	**−.73**	−.12	−.08	.69
Innovative	.13	.07	**.71**	.18	.02	.56
Distractable	−.27	.14	**.68**	−.02	.09	.57
Inventive	.26	.28	**.65**	.15	−.08	.60
Erratic	−.20	.15	**.60**	−.22	**.41**	.64
Individualistic	**.44**	−.20	**.56**	−.28	.08	.64
Impulsive	.06	.36	**.56**	.16	.52	.74
Excitable	**−.48**	**.44**	**.53**	−.07	.18	.74
Disorganized	**−.44**	.22	**.47**	.19	.11	.51
Helpful	.24	.06	.00	**.90**	.10	.87
Affectionate	−.10	.20	−.03	**.84**	−.22	.80
Sympathetic	−.03	−.25	.07	**.83**	−.20	.80
Sociable	.24	**.45**	.19	**.72**	.05	.81
Friendly	−.20	.30	−.08	**.70**	**−.41**	.79
Solitary	−.20	**−.53**	−.20	**−.63**	−.05	.77
Curious	.06	**.44**	**.55**	**.63**	.12	.91
Inquisitive	−.01	.34	**.45**	**.62**	.26	.76
Sensitive	−.07	.04	−.08	**.60**	.14	.40
Jealous	.25	−.12	−.14	.05	**.83**	.79
Stingy/greedy	.20	−.24	−.22	.04	**.82**	.81
Bullying	.31	.23	.26	−.10	**.78**	.84
Aggressive	.37	.15	.29	−.04	**.77**	.83
Irritable	−.11	.29	.37	−.19	**.73**	.79
Manipulative	**−.54**	.03	.18	.12	**.64**	.74
Gentle	−.23	**−.41**	.08	.53	**−.60**	.86
Defiant	.16	**.44**	**.47**	.03	**.50**	.69
Imitative	−.39	.32	−.12	−.04	−.17	.29
Autistic	−.07	.11	−.19	−.32	.24	.21

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Tonkean macaques *(Macaca tonkeana)*

Because there were fewer subjects (46) than items (54), we conducted a principal components analysis of a correlation matrix smoothed to the nearest positive definite matrix (Wilson, de Boer, Arnott, & Grimmer, 2011). A parallel analysis indicated a 5-component structure (eigenvalues = 26.1, 16.5, 5.7, 3.8, 3.3). However, the 5-component introduced moderate correlations (.30-.39) among loadings of three of the components. We therefore extracted four components (Table S5).

The first component was defined by item loadings related to agreeableness (*dominant, bullying, submissive*) and neuroticism (*fearful*, *timid*), indicating it characterized variation in social competence. This dimension had salient loadings from items related to aggression (*aggressive, bullying*) and was marked by items indicating low conscientiousness (*reckless*, *impulsive*). Domain scores were highly correlated with scores on rhesus Dominance and Confidence and with the ape Dominance dimensions. It did not correlate as strongly with the other species' Anxiety and Neuroticism domains but did have a strong negative correlation with chimpanzee Conscientiousness. We labeled it 'Dominance.'

The second component was characterized by items suggesting that animals high on this trait would be active, playful, and explorers of their environment. Scores on this domain correlated highly with the Openness dimensions of the comparison species as well as with chimpanzee and Orangutan Extraversion. We called this domain 'Openness.'

Items that had a high loading on the third component indicated that this dimension characterized differences in social affiliation. Domain scores correlated strongly with scores on rhesus Friendliness and with chimpanzee and orangutan Agreeableness and, to a lesser extent, Extraversion. We labeled this factor 'Friendliness.'

The last component was defined by items on the low pole of extraversion (*solitary, depressed*) and was similar to the third component in describing differences in social style. Individuals scoring high on this domain would tend to act independently of the actions of others. Scores were had a negative correlation with rhesus macaque Friendliness and the ape Extraversion domains. It differed from Friendliness by not having primary loadings from items related to agreeableness. It therefore seemed to represent a separate sociable-solitary axis, similar to the Connectedness dimension in crested macaques (Neumann, Agil, Widdig, & Engelhardt, 2013). We reflected the loadings on this component and labeled it Sociability.

Table S5: Tonkean macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings (≥|.40|) are bolded. Dom = Dominance, Opn = Openness, Frd = Friendliness, Soc = Sociability. h^2 = communalities.

	Dom	Opn	Frd	Soc	h2
Stingy	**.94**	.10	−.02	−.01	.89
Persistent	**.93**	−.04	−.02	−.14	.90
Vulnerable	**−.93**	.10	.13	−.10	.90
Timid	**−.92**	.02	.13	−.22	.91
Dominant	**.90**	−.26	−.14	−.03	.90
Cautious	**−.89**	−.20	.18	−.04	.87
Submissive	**−.88**	.07	.07	−.09	.79
Decisive	**.87**	.03	.19	−.09	.81
Bullying	**.86**	.22	−.11	−.18	.84
Fearful	**−.84**	.13	.11	.01	.73
Aggressive	**.84**	.24	−.15	−.10	.79
Jealous	**.74**	**.43**	.08	−.12	.75
Irritable	**.70**	.33	−.12	−.21	.65
Reckless	**.65**	.63	.17	−.13	.86
Anxious	**−.64**	.31	.07	−.01	.52
Defiant	**.61**	**.53**	.18	−.09	.69
Curious	**.54**	**.54**	**.42**	−.05	.77
Quitting	−.39	−.06	−.30	.13	.26
Active	.03	**.92**	.20	.13	.90
Lazy	.22	**−.86**	.02	−.14	.81
Playful	−.06	**.80**	.32	.07	.75
Conventional	−.13	**−.80**	−.12	−.10	.68
Excitable	.37	**.79**	.03	.08	.77
Predictable	−.06	**−.77**	−.11	−.14	.63
Inquisitive	.29	**.74**	.19	−.01	.67
Impulsive	**.50**	**.70**	.07	−.06	.76
Innovative	.23	**.70**	.34	−.34	.77
Inventive	.29	**.68**	.35	−.28	.75
Thoughtless	**.60**	**.67**	.11	−.08	.83
Stable	**.45**	**−.66**	.21	−.06	.68
Distractable	−.03	**.65**	−.18	.16	.48
Unemotional	.06	**−.64**	−.33	−.36	.66
Imitative	−.13	**.63**	−.18	.15	.47
Erratic	**.41**	**.63**	.03	−.06	.57
Cool	.11	**−.58**	.23	−.12	.42
Manipulative	**.55**	**.58**	−.09	−.09	.65
Disorganized	−.21	**.56**	.07	−.05	.37
Helpful	−.12	−.03	**.89**	−.04	.80
Sympathetic	−.12	.09	**.87**	.08	.78
Sensitive	−.16	.06	**.80**	.13	.68
Sociable	.18	.38	**.69**	**.51**	.91

Affectionate	−.29	.16	**.67**	**.55**	.86
Gentle	**−.53**	−.10	**.65**	.26	.78
Intelligent	**.42**	.27	**.52**	−.31	.61
Clumsy	−.15	.02	**.46**	**−.40**	.40
Solitary	−.06	**−.45**	−.11	**−.78**	.82
Individualistic	.39	.03	−.10	**−.72**	.69
Friendly	−.13	.33	**.56**	**.67**	.89
Depressed	−.36	−.34	.05	**−.66**	.69
Independent	**.51**	−.35	−.23	**−.66**	.87
Autistic	.06	.14	.16	**−.61**	.42
Dependent	−.35	**.48**	.35	**.61**	.84
Protective	.28	−.26	.37	**.52**	.55

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Crested macaques (Macaca nigra)

Because the crested macaque sample had the same number of subjects (53) as reliable items (53) we checked that the item correlation matrix was positive definite and found that it was (Wilson, de Boer, Arnott, & Grimmer, 2011). A parallel analysis indicated a 4-component structure (eigenvalues = 14.8, 7.6, 7.2, 3.4) (Table S6).

The first component contained items related to agreeableness (*sympathetic, protective, helpful*), extraversion (*sociable, solitary*), and openness (*inquisitive, curious*). Scores on this trait were highly correlated with rhesus Friendliness and the ape species' domains of Extraversion and Agreeableness. Scores were also correlated with scores on the other species' Openness domains. However, because it correlated almost perfect with rhesus Friendliness, we also labelled this component 'Friendliness'.

The second component was defined by markers of neuroticism (*fearful, anxious*) and agreeableness (*dominant, submissive*). It did not contain items more directly related to depression, which instead loaded on the third component. This domain was thus similar to rhesus Confidence. We labelled this component 'Confidence'.

The third component contained items related to aggressive (*bullying*, *aggressive*) and erratic (*reckless, excitable).* Individuals scoring high on this dimension would likely be aggressive, uncooperative, and unpredictable. This component differed from the rhesus Dominance domain in not having items related to social competence and was therefore more like the Opportunism dimension found in Assamese macaques. Scores on this component correlated positively with scores on rhesus Dominance and Anxiety domains and negatively with the chimpanzee Conscientiousness domain. We labelled this component 'Aggressiveness'.

The fourth and final component contained items related to low agreeableness (*manipulative, individualistic*) and high anxiety (*excitable,* not *unemotional*). Scores on this domain did not correlate strongly with scores on any of the chimpanzee domains and scores were most similar to those on chimpanzee Neuroticism. Individuals scoring high on this domain would likely have high emotional reactivity. We labelled this component 'Excitability'.

Table S6: Crested macaque personality domain loadings from a principal components analysis using orthogonal rotation. Salient loadings (≥|.40|) are bolded. Frd = Friendliness, Cnf = Confidence, Agg = Aggressivness, Exc = Excitability. h^2 = communalities.

	Frd	Cnf	Agg	Exc	h2
Sympathetic	**.90**	.02	−.07	−.19	.86
Friendly	**.88**	.07	−.15	−.19	.84
Affectionate	**.84**	.06	−.14	−.13	.75
Sociable	**.81**	.19	.24	.01	.74
Playful	**.78**	.13	.29	−.08	.72
Protective	**.78**	.27	.09	−.14	.71
Helpful	**.77**	.05	−.11	−.08	.61
Solitary	**−.70**	−.32	−.39	.08	.75
Sensitive	**.70**	.01	−.02	−.24	.54
Lazy	**−.63**	−.36	−.32	−.10	.64
Imitative	**.61**	−.08	.14	.18	.43
Inquisitive	**.60**	.31	**.47**	.02	.68
Curious	**.57**	.38	**.48**	.13	.72
Active	**.54**	**.43**	**.51**	.12	.75
Unperceptive	−.34	−.33	.08	.26	.30
Fearful	−.08	**−.90**	.00	−.17	.85
Dominant	.01	**.87**	.18	.13	.81
Vulnerable	−.10	**−.84**	.05	−.14	.74
Timid	−.35	**−.77**	−.25	.18	.81
Independent	.00	**.75**	−.02	.06	.57
Cool	.09	**.72**	−.35	−.19	.69
Submissive	−.13	**−.71**	−.18	−.08	.56
Anxious	**−.49**	**−.70**	.03	.10	.74
Intelligent	.25	**.66**	.04	−.03	.50
Persistent	.21	**.62**	.35	.09	.56
Depressed	−.22	**−.56**	.00	**−.46**	.57

Clumsy	−.14	**−.55**	.19	.21	.41
Stingy	.29	**.52**	**.46**	−.25	.63
Dependent	.39	**−.46**	−.04	.00	.37
Quitting	.02	**−.44**	.25	**−.44**	.45
Autistic	.07	**−.40**	−.14	.23	.24
Erratic	.28	−.18	**.80**	−.01	.75
Gentle	.19	.08	**−.79**	.07	.67
Reckless	**.44**	.24	**.74**	−.14	.82
Defiant	.37	.19	**.72**	−.19	.73
Distractable	**.40**	−.09	**.70**	−.19	.69
Bullying	−.29	.29	**.67**	.15	.65
Disorganized	.27	−.33	**.65**	.03	.60
Jealous	.32	**.47**	**.63**	.04	.72
Irritable	.05	−.10	**.63**	−.28	.49
Aggressive	−.27	.37	**.62**	.28	.66
Excitable	.09	−.30	**.58**	**.51**	.69
Cautious	.12	−.23	**−.47**	−.05	.29
Stable	.36	.45	**−.47**	−.34	.67
Predictable	.17	.04	−.38	−.25	.24
Unemotional	.10	.36	.12	**−.78**	.76
Decisive	−.13	**.46**	−.22	**.66**	.71
Manipulative	−.15	**.48**	.15	**.63**	.67
Individualistic	−.36	.00	−.04	**.62**	.52
Conventional	**.55**	.02	−.08	**−.61**	.67
Impulsive	.12	−.09	**.55**	**.59**	.67
Innovative	.32	.30	.32	**.50**	.55
Thoughtless	.30	.08	.19	**−.39**	.28

Other species comparisons

Table S7: Correlations between unit-weighted scores for macaques as defined by the species structures and rhesus macaque and chimpanzee structures. Bold indicates significance at p<.001. Anx = Anxiety, Act = Activity, Cnf = Confidence, Dom = Dominance, Ext = Excitability, Frd = Friendliness, Irr = Irritability, Opn = Openness, Opp = Opportunism, Soc = Sociability

	Japanese macaque				Barbary macaque				Assamese macaque					Tonkean macaque				Crested macaque			
	Dom	Opn	Frd	Anx	Cnf	Opn	Frd	Irr	Cnf	Act	Opn	Frd	Opp	Dom	Opn	Frd	Soc	Frd	Cnf	Agg	Exc
Rhesus																					
Dom	**.82**	**.58**	-.27	.03	**.67**	.09	.39	**.50**	**.68**	.28	**.50**	.06	**.91**	**.95**	.36	-.17	-.28	.27	**.59**	**.77**	.39
Cnf	**.89**	-.01	.20	**-.49**	**.98**	**-.47**	.14	-.13	**.94**	-.04	-.22	.09	.34	**.86**	-.13	-.28	-.27	.20	**.86**	-.14	.09
Frd	**.45**	.35	**.84**	-.39	**.61**	-.06	**.64**	**-.65**	.42	**.54**	.15	**.93**	.16	.25	.42	**.79**	**.77**	**.97**	**.52**	.20	-.25
Opn	.33	**.94**	.22	.19	-.24	**.94**	**.53**	.11	.11	**.74**	**.82**	**.65**	.39	**.55**	**.90**	.28	.14	**.78**	.40	**.63**	.15
Anx	-.32	.33	**-.46**	**.58**	**-.72**	**.67**	.18	.35	**-.44**	.42	**.60**	.06	.39	.17	**.74**	.25	.33	-.06	**-.51**	**.62**	.24
Act	.20	**.75**	.25	.00	.06	**.63**	**.82**	-.07	.01	**.94**	**.60**	**.54**	.11	.11	**.91**	.25	.43	**.66**	**.52**	**.45**	.19
Chimpanzee																					
Dom	**.99**	.36	.05	-.20	**.98**	-.28	.27	.02	**.93**	.20	.21	.20	**.72**	**.98**	.14	-.23	-.29	.30	**.91**	.39	.29
Ext	.30	**.61**	**.75**	-.10	.21	**.50**	**.92**	-.35	-.02	**.85**	.39	**.86**	.01	.06	**.79**	**.56**	**.80**	**.97**	.48	.35	-.14
Agr	.23	.26	**.85**	-.31	.38	-.29	.20	**-.92**	.27	-.03	-.15	**.70**	-.14	-.18	.01	**.91**	**.51**	**.85**	.25	-.07	-.38
Neu	-.07	.24	**-.62**	.08	**-.70**	**.47**	.19	.37	-.12	**.83**	**.72**	.32	.41	.04	**.84**	.26	.47	-.21	-.38	.38	**.62**
Opn	.24	**.86**	.37	.06	-.09	**.78**	**.42**	-.10	.20	**.69**	**.68**	**.75**	.31	.40	**.84**	.27	.14	**.72**	**.51**	**.55**	.04
Con	-.28	**-.74**	.34	**-.54**	.25	**-.87**	**-.40**	**-.49**	-.16	**-.57**	**-.84**	-.25	**-.72**	**-.68**	**-.78**	-.23	.06	**-.44**	-.10	**-.96**	-.06
Orangutan																					
Ext	.29	**.82**	.28	-.01	.01	**.78**	**.83**	-.01	-.01	**.95**	**.60**	**.64**	.21	.14	**.90**	.24	**.54**	**.68**	**.50**	**.54**	.38
Dom	**.90**	**.57**	-.13	-.04	**.77**	-.01	**.40**	**.40**	**.72**	.28	.38	.09	**.94**	**.97**	.35	-.14	.17	.41	**.66**	**.77**	.16
Agr	.30	.38	**.86**	-.26	**.42**	-.01	**.60**	**-.78**	.29	.40	.02	**.90**	.03	-.03	.27	**.88**	**.77**	**.93**	.30	.10	-.35
Neu	**-.68**	.17	**-.46**	**.63**	**-.92**	**.50**	-.09	.29	**-.71**	.26	**.49**	-.09	.02	**-.56**	.47	.28	.27	-.30	**-.78**	.32	.22
Int	**.78**	.20	.20	**-.64**	**.81**	**-.67**	-.08	-.17	**.91**	-.05	-.10	-.06	.37	**.65**	-.20	-.37	**-.61**	.06	**.79**	-.25	.22

Factor score reliabilities

Table S8: Interrater reliabilities (ICC[3, 1] and ICC[3, *k*]), and internal consistencies (Cronbach's alpha) of personality and subjective well-being domains scores.

	ICC(3, 1)	ICC(3, *k*)	α
Japanese macaque			
Dominance	.67	.74	.92
Openness	.61	.68	.90
Friendliness	.37	.45	.87
Anxiety	.73	.79	.89
Barbary macaque			
Confidence	.44	.65	.96
Openness	.44	.65	.94
Friendliness	.59	.78	.87
Irritability	.37	.58	.84
Assamense macaque			
Confidence	.60	.89	.94
Activity	.51	.85	.90
Openness	.27	.68	.88
Friendliness	.38	.77	.90
Opportunism	.32	.72	.91
Tonkean macaques			
Dominance	.62	.87	.97
Openness	.61	.86	.95
Friendliness	.53	.82	.87
Sociability	.54	.82	.87
Crested macaques			
Friendliness	.77	.87	.94
Confidence	.70	.83	.92
Aggressivness	.41	.59	.91
Excitability	.58	.74	.80

Fuzzy set item membership

Table S9: Membership of items in fuzzy intersections of personality domains for the five macaque species. Membership values have been reassigned their positive and negative valence so that the direction of the loading can be interpreted. *D* = dominance, *C* = confidence, *F* = friendliness, *O* = openness, *G* = aggressiveness, *I*= irritability, *X* = anxiety, and *P* = opportunism. K_r = rhesus macaque, K_j = Japanese macaque, K_b = Barbary macaque, K_a = Assamese macaque, K_t = Tonkean macaque

Confidence–M

$$C_M = C_r \cap D_j \cap C_b \cap C_a \cap C_c \cap D_t$$

Item	*m*(*i*)
Fearful	−.73
Submissive	−.71
Timid	−.67
Dominant	.50
Anxious	−.41
Vulnerable	−.40
Dependent	−.35
Depressed	−.32
Decisive	.30
Cautious	−.22
Disorganized	−.21

Dominance–M

$$D_M = D_r \cap D_j \cap C_b \cap C_a \cap C_c \cap D_t$$

Item	*m*(*i*)
Dominant	.64
Vulnerable	−.54
Independnet	.51
Manipulative	.46
Decisive	.46
Submissive	−.43
Aggressive	.35
Dependent	−.35
Bullying	.28
Protective	.27
Anxious	−.26
Jealeous	.23
Depressed	−.22
Cautious	−.22
Timid	−.22
Disorganized	−.21
Fearful	−.21
Stingy	.20

Friendliness–M

$$F_M = F_r \cap F_j \cap F_b \cap F_a \cap F_c \cap F_t$$

Item	$m(i)$
Sociable	.65
Affectionate	.55
Friendly	.49
Curious	.33
Helpful	.27

Aggressiveness–M

$$G_M = D_r \cap D_j \cap I_b \cap P_a \cap G_c \cap D_t$$

Item	$m(i)$
Bullying	.63
Aggressive	.50
Defiant	.37
Irritable	.36
Jealous	.30
Stingy	.30
Impulsive	.26
Gentle	–.25

Anxiety–M

$$X_M = X_r \cap X_j \cap C_b \cap C_a \cap C_c \cap D_t$$

Item	$m(i)$
Anxious	.60
Vulnerable	.41
Quitting	–.39
Fearful	.34
Independent	–.27

Openness–M

$$O_M = O_r \cap O_j \cap O_b \cap O_a \cap F_c \cap O_t$$

Item	$m(i)$
Playful	.49
Conventional	–.46
Inquisitive	.45
Reckless	.35
Innovative	.30
Thoughtless	.30
Curious	.30
Active	.28
Erratic	.25
Defiant	.25

Source code.

Code for the fuzzy set analysis is available as an R package from `https://github.com/mja/fuzzymonkey` and also includes data for the personality structures of the 5 species that are new to this study. The code can be installed using the `devtools` package

```
library(devtools)
install_github('fuzzymonkey', 'mja')
library(fuzzymonkey)
```

A sample analysis can be conducted by importing the personality loadings matrices for Japanese (M. fuscata), Barbary (M. sylvanus), Assamese (M. assamensis), crested (M. nigra) and Tonkean (M. tonkeana) macaques

```
data(fuscata)
data(sylvanus)
data(assamensis)
data(nigra)
data(tonkeana)
```

The function fuzzy_intersect() takes an arbitrary number of vectors of item loadings labelled with item names (labelling will occur automatically when extracting columns from FA and PCA loadings matrices or from matrix objects with labelled rows). For example, to find the fuzzy intersection of the Dominance/Confidence components from each personality structure:

```
fuzzy_intersect(fuscata[,1], sylvanus[,1], assamensis[,1],
nigra[,2], tonkeana[,1])
```

```
 Fear     Tim     Dom    Subm     Anx    Vuln    Indp    Manp    Decs    Pers
-0.804  -0.768   0.766  -0.710  -0.561  -0.553   0.510   0.463   0.457   0.450
 Intll    Quit    Aggr    Depd    Depr    Buly    Prot   Jeals    Caut    Dsor
 0.418  -0.388   0.348  -0.348  -0.323   0.278   0.266   0.226  -0.218  -0.211
 Stngy     Soc    Defn    Exct    Cool   Reckl    Irri    Gntl    Invt    Impl
 0.204   0.179   0.158   0.132   0.115   0.113  -0.107   0.089   0.063   0.062
  Pred    Stbl Curious     Aut   Innov    Unem     Sol    Help    Lazy    Imit
-0.061   0.060   0.060   0.059   0.057   0.057  -0.056   0.049  -0.040  -0.035
  Errc    Dist    Conv    Affc    Symp    Sens    Frdy    Inqs   Thotl    Clmy
 0.032  -0.031   0.031   0.027   0.026   0.014   0.012  -0.010   0.008  -0.007
 Unper    Indv    Actv    Play
-0.006  -0.005   0.001   0.000
```

This shows that the fuzzy intersection consists of the items Fearful (-0.804), Timid (-0.768), Dominant (0.766), Submissive (-0.710) at so on.

References

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